BROOKLYN BOTANIC GARDEN

MEMOIRS

VOLUME II

THE VEGETATION OF LONG ISLAND

PART I

THE VEGETATION OF MONTAUK

A STUDY OF GRASSLAND AND FOREST

BY

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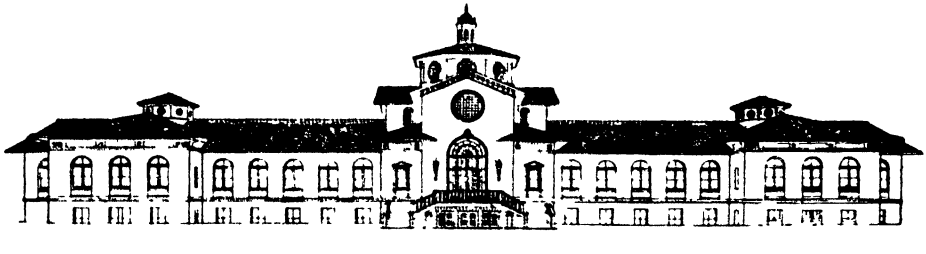

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PREFACE.

This is the first of a series of papers on "The Vegetation of Long Island," which it was intended should be issued under one cover. To issue them as separate parts, as they are completed, now seems the better plan as not much has ever been written on this phase of Long Island plant life, and practically nothing at all upon the environmental factors which determine it.

Studies of the well-nigh world wide contest between grassland and forest are so common that it should be said that the peculiar climatic and topographic conditions at Montauk alone make necessary the publication of another such paper. As will be seen, the response of the vegetation at Montauk is in many ways unique.

The attempt to put into plain English what appears to be the vegetative history of Montauk, without using the multitude of terms that etymologically adroit ecologists have given us, may seem to demand some apology from my colleagues. But a glance at recent ecological literature shows that many of these terms are not yet free from confusion or controversy, whereas English still possesses the incomparable advantage of being understood not only by most ecologists, but by others.

In gathering instrumental data, in the identification of critical species, and in other ways, I have had assistance from various people whose special services are acknowledged in the different sections of the book. I am particularly pleased to make grateful acknowledgment to my friend and colleague, Major Barrington Moore, who has shown constant interest and helpfulness during the work, and especially during several trips to Montauk. To my assistant Helen Smith Hill I am under great obligation foı efficient help in carrying through most of the details of instrumental work, of experimental cultures for testing the moisture-holding capacity and wilting coefficient of many soil samples, and in many other ways. The photographs, except where noted otherwise, were taken by the writer.

NORMAN TAYLOR.

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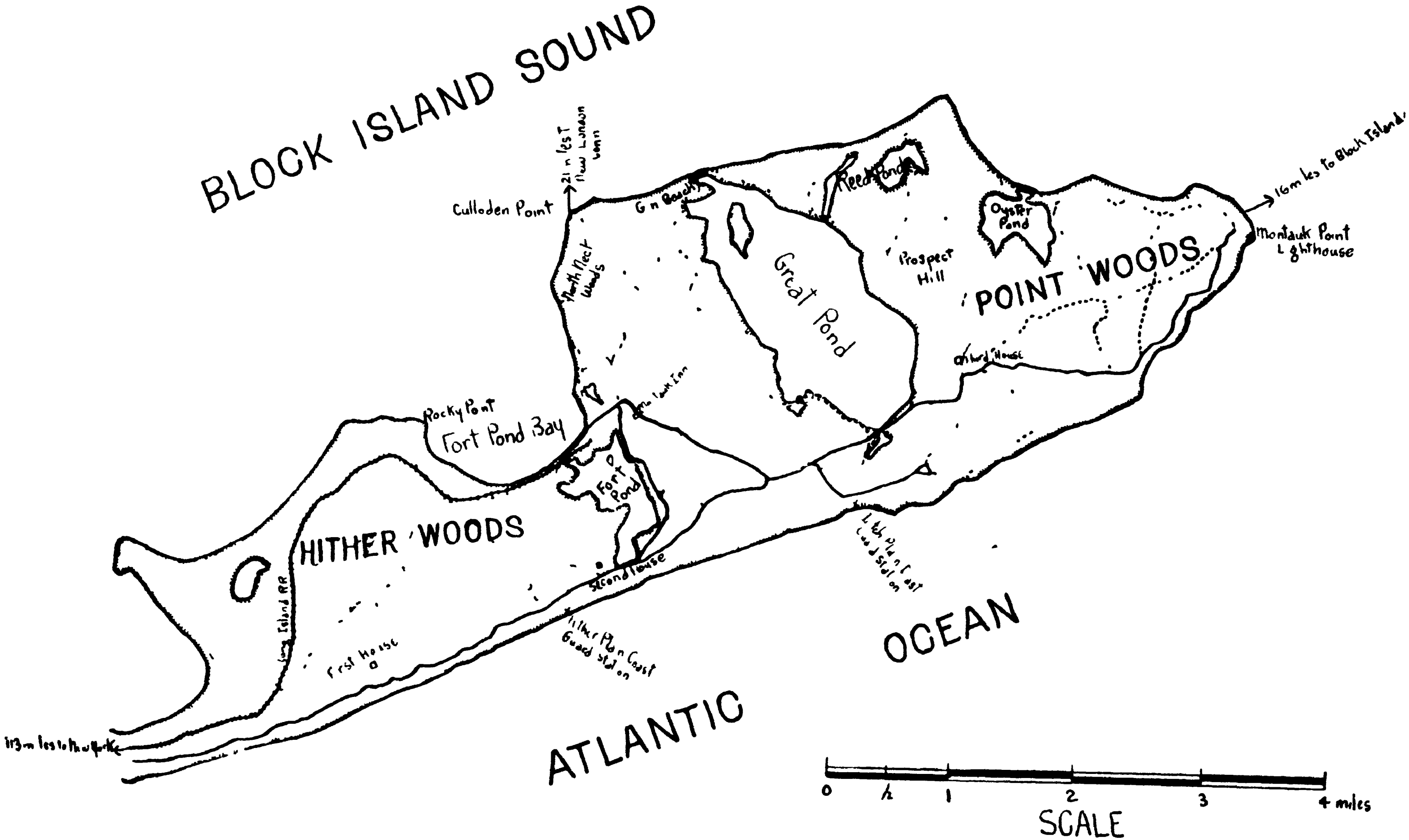


FIGURE 1. Map of Montauk, showing principal roads, trails, coast guard stations, lighthouse and other features. See Figure for condensed panorama of the region from the Inn eastward.

MONTAUK AND ITS TOPOGRAPHY.

One hundred and thirteen miles from New York on the eastern extremity of the south fluke of Long Island is the peninsula of Montauk, famous since 1640 when Captain Lion Gardiner founded Easthampton, the present township of which includes Montauk.

In approaching it by train from New York, one passes, during the last few miles of the ride, through an apparently ancient oak forest, about four miles in extent, known from the earliest days as the Hither Woods. Quite suddenly the train debouches from these woods onto the open Downs, skirting the edge of a beautiful crescent bay, upon the beach of which the fishing hamlet of Montauk is picturesquely scattered. This tiny village, largely depopulated of its fishermen in the winter, is the last station on the railroad, and is seven miles by road from the lighthouse at Montauk Point, which is the easterly extremity of New York State.

The topography of Montauk is dominated by the kettleholes, and the areas between them, which in the case of treeless sections are known as The Downs, and give the whole Point a characteristic aspect. For miles one sees nothing but rolling hills, deceptive as to size and the depth of the kettleholes between them, mostly bare of trees, from the easterly edge of the Hither Woods, to just east of Great Pond.

J. A. Ayres who visited Montauk, and wrote an account of it in 1849, writes of the general aspect of the place as follows:

"Southeast, we have a very fair representation of the *hills of Montauk*. Of these hills it is almost impossible to convey a correct idea. Rounded and rolling, but in many cases quite steep and abrupt, not arranged in ridges, but scattered apparently at random; with no level land among them, but deep cup-shaped hollows seeming like reversed copies of the hills themselves; bare of trees and covered only with a smooth turf, as close as though it had been shorn, their appearance is *sui generis*. We cannot place ourselves on any part of the extent which bears the name Montauk, without fully understanding the propriety of the name. It is in truth a "Hilly Land." From Nommonock to Wamponomon* the rolling surface is unbroken, except by the ponds and one or two small spaces which are by courtesy called plains. The highest of these hills, in the western part of the peninsula, are those on which we are standing."

* Old names for the hills just east of Napeague, and for the "Turtle Hills" on which the Lighthouse now stands at the extreme Point.

The bottoms of four of these kettleholes are permanently occupied by water, viz.: Fort Pond, near the town; Great Pond,* the largest lake on Long Island, with a very considerable island near one end of it; Reed Pond which is little more than an offshoot of Great Pond; and Oyster Pond, the most easterly of all. Both the latter are small bodies of water, Great Pond is about two miles long and one wide, comprises 1300 acres, and occupies most of the center of the Point, while Fort Pond is of irregular shape and is about a mile in its longest dimension.

The kettleholes occupied by these ponds are the largest on the Point, most of the others not exceeding 6 to 8 acres, and scores of them only a few square rods in extent. Those kettleholes without ponds in them show all gradations between practical dryness and a water table that is only just above or beneath the surface. The nearness of this water table to the bottom of the kettlehole is reflected in the type of vegetation now found in them, or that is developing in some of those whose progression from early stages to final vegetative covering is still under way.

* Called in most old records and on some modern maps Lake Wyandannee. So in Dr. Dickinson's panorama, figure 2.

HISTORY OF THE POINT AND EARLY CONDITION OF ITS VEGETATION.

Casual visitors to Montauk are charmed by the wildness of the place, the desolate moor-like Downs, the depths of the kettleholes, some destitute of woody vegetation, others dark and even mysterious in their wooded interior. The feeling that the vegetation has always been so, and that from the earliest times the Indians, whose relics are common enough on the Point, must have roamed through a region such as our modern pedestrian sees, is natural enough.

While this may not be wholly true, it appears from a study of the records* of the earliest settlers that there has always been, within historic times at least, a distinct separation of grassland and woodland. While not necessarily of the same extent today as when the Indians of Montauk agreed with the settlers of Easthampton, on May 22, 1658, as to the use of the Point, there can be little doubt that some forest land, certainly the Hither Woods, and great areas of grassland, such as characterize it today, covered large areas.

In this first written agreement between Wyandanch, the chief of the Montauk Indians, and the settlers of Easthampton, it is stated that the latter had granted to them the privilege of "pasturing their cattle on Montaukett (the old name) for seven years." At the end of that period, and after his death, his daughter, Sunk-squa, made the following agreement with Easthampton on October 4, 1665.

"1. The bounds of the town east to the Fort-pond, and all the rest to the end of the island, to belong to the Indians; but not to be disposed of to any other than the people of the town.

"2. The inhabitants forever to have full and free liberty at any time to cut *grass on said lands*, and for feeding of cattle, but not till the corn, planted by the Indians, shall be taken off.

"3. If cattle trespass on the Indians, by reason of not keeping up the fence, the town to make satisfaction; and if Indian dogs do damage to cattle, they to make satisfaction.

* I am glad to make acknowledgment here for the use of the admirable collections of the Long Island Historical Society, which have been diligently searched for authentic records of the early condition of the vegetation, not only of Montauk, but of other parts of Long Island. To Miss Emma Toedteberg, the librarian, I am particularly grateful for making many helpful suggestions in the course of this part of the work.

"4. Indians not to set *fire to the grass* before the month of March, without consent of the town. In consideration of all which, the town engages to pay, yearly 40 shillings to said Sunk-squa and Indians, their heirs and assigns.

"Made and agreed to before me, Richard Nicoll.

"Matthias Nicoll, *Sect'y*."

The italics are mine.

As the town of Easthampton, which included all of Montauk, was settled in 1640, it is thus only twenty-five years later that the management of the peninsula becomes a matter of record, between the settlers and the Indians, who were friendly.

These records show that there was evidently a very considerable part of the peninsula in grassland at that time, but as to woodland, it is not so clear. There are, however, frequent references in these old records to the Hither Woods, which still exists at about the place designated in these early chronicles.

By the end of the century conditions at Montauk needed to be redefined and a new agreement was entered into between the Indians and the town of Easthampton. It gives us such a good picture of conditions in 1702, or sixty years after the first whites came to that end of Long Island that it is inserted here complete.

"The said Indians are to fence in as a general field what land they see cause upon the Northneck [near Culloden Point] which lies between the Fortpond to the westward and the Greatpond to the eastward, for their planting field; and wholly to leave the land to the eastward of the Greatpond unto the English; and the said Indians shall from year to year lay and keep open their field or fields for the said town's cattle to feed upon (excepting only some small fields which they may keep inclosed for winter wheat or grass not exceeding thirty acres;) and the time of the said field or fields shall be laid open is to be upon the tenth or fifteenth of October, and so to continue open until the twenty fifth day of April after. The said Indians making and continually keeping and maintaining a good sufficient fence about all their fields at their own expense, cost and charges.

"That if the said Indians or their posterity as long as they live upon Meantauk [another old spelling] shall cause to leave that field and remove to the eastward of the said Greatpond, then they shall wholly quit the Northneck, and shall have liberty to fence in a field from the southwardmost part of the Greatpond running southward to a small round swamp near the dich bars; [the present Ditch Plain] and so from thence to run in at the southeast part of the oyster pond; and to plant and improve the land on the northward part of the said line of fence; and they and their posterity after them shall have liberty, as often as they see cause, to exchange their field from one side of the said Greatpond to the other; still sufficiently

fencing their fields at their own costs and charges, and observing the rules of laying them open as is before prescribed.

"And the said Indians and their posterity shall have liberty to keep upon the said land two hundred and fifty swine, great and small; the said Indians paying all such damage to the English as they shall sustain by the rooting of the said swine; and to keep horse kind and neat cattle not exceeding the number of fifty in all, and to get hay to winter them; but they are not to take any horse kind, cattle or swine to keep for any other person, nor to sell, give or any way dispose of any grass or hay to any person whatsoever; nor shall they have liberty to permit or let out any land to any person, either to plant, sow, or any other way to improve.

"That the said Indians and their posterity after them shall have liberty to make use of so much of that timber of the town on this [west] side of the Fortpond [the Hither Woods] as they shall need to fence in their general field, after they have used all the fencing stuff that is upon the Northneck, if the English do not lay out that land into parcels or lotments and improve the same. In testimony hereof, we the parties to these presents have hereunto set to our hands and fixed our seals enterchangeably, this 3rd day of March 1702/3."

From this it appears that there was certainly both timber and grassland at Montauk, both east and west of Great Pond, but ten years later there can be no doubt about the shortage of timber, for records of the town of Easthampton, dated April 7, 1713, have this to say about the question;

"Also in regard of the scarcity for timber at Montauk for the enclosures and for the prevention of its being destroyed or improved to wrong uses, it is ordered by the said Trustees that whosoever shall presume to fell or cut down tree or trees standing on any part of Mentauk [another old spelling] or carry or any way bring off from Mentauk any part of its growth by land or water except such as have authority so to do by virtue of some former deed or contract or by permission from the Trustees for the time being, he or they for so offending shall forfeit to the use of said Trustees for each and every tree felled or cut down aforesaid the sum of ten shillings and for each and every load of timber any way carried off as aforesaid the sum of forty shillings."

At the end of the year, in casting up the accounts of expenses of Montauk, which was a common pasturage, appear two significant items, thus:

	s.	d.
To Jeremiah Miller for carting 1,000 feet of boards to Montauk............	5	6
To Stephen Leek for carting 2,000 feet of boards to Montauk...........	13	0

In fact in 1676 there were already signs that our ruthless ancestors began to see where their methods would lead them, for David Gardiner in his "Chronicles of the Town of Easthampton" says:

"The rapid diminution of timber had attracted attention as early as 1676, when at a Court of Sessions held at Southold, by his Majesty's

authority, it was ordered 'that no person not having an allotment and thereby a right in the commons should cut timber in Easthampton.' It now became necessary to provide against the frequent fires, which were found more destructive than the trespasses of individuals, and in 1710, the Trustees were authorized to call out the inhabitants to assist in extinguishing them. Upon the erection of the church a few years afterwards, it was found necessary to resort to Gardiner's Island for timber of sufficient size for the frame."

Besides this unmistakable evidence of the presence of forest, the protection of which had already become a matter of concern, the village records give us many hints of the importance of the grassland at Montauk. On June 20, 1744, they authorized "Captain Baker to build a house for the shepherds west of Fort Pond." And forty-three years later there appeared in the town records the following, under date of January 22, 1787. (Records of the Town of Easthampton **6**: 252. 1889.).

"1st. That all the hither end of Montauk west of the fort pond, shall be improved, to keep sheep for the benefit of the proprietors, and that all the cattle and horses shall be kept to the eastward of the said fort pond.

2d. That sixty-four sheep shall be allowed to go on one whole share, and in the same proportion for a greater or less right, and that four sheep shall go on and be entered in lieu of one neat beast, and that the lambs shall be entered on right, the same as grown sheep, by the first Wednesday in November, or be liable to poundage as grown sheep, and that all sheep that shall be found grazing on said land of Montauk not having right or not being duly entered, shall be impounded, the owner or owners of all such sheep so impounded paying two shillings for each sheep so impounded."

During the Revolution we get a vivid picture of the amount of grazing for on July 5, 1775, "The people of East and Southampton pray Congress that Captain Hurlbert's company, now raising for Schuyler's army, may remain to guard the stock on the common lands of Montauk (2,000 cattle and 3 or 4,000 sheep) from the ravages of the enemy." This was granted by Congress on July 31, 1775, but in spite of it the British took the cattle from Montauk on August 23, 1779.

That there may have been forests at Montauk greater than those found at the present time is indicated by Thompson in 1839, in the first volume of his "History of Long Island' (page 307) where he says: "[The] Peninsula of Montauk, containing as it does more than 9,000 acres, constitutes a considerable portion of the town (Easthampton). The timber once so abundant has now greatly depreciated." Such records of Thompson, and they have many times been repeated by Prime, Furman, Ross, Gabriel and other historians of Long Island, may be more true than they realized. While within *historic* times there is scarcely any evidence of great changes, as to

the distribution of grassland and forest at Montauk, there may well have been much greater areas of forest in pre-historic days. Further details of this will be found in the summary.

Not only the disturbance of the vegetation in the seventeenth and eighteenth centuries, and the grazing which has continued ever since (now much reduced in volume from what it was during the Revolution) but still another upheaval of the vegetation occurred during the Spanish-American war in 1898. At that time thousand of troops were quartered there and practically all the land between Fort and Great Pond was covered with troops and their equipment. It was also used as an aviation station during the Great War, but, so far as disturbance of the vegetation is concerned, on a much reduced scale. During 1921 and 1922, however, part of the area east of Fort Pond was used as a training ground for artillery regiments, whose manoeuvering and shooting destroyed large tracts of the Downs vegetation.

Montauk is a region, then, that has been through many phases in the disturbance of its vegetation, and in interruptions to the natural fulfillment of its vegetative destiny. This is now going on, in some places rapidly, and in others hardly at all, as the sequel will attempt to show. One interesting fact about the vegetation of the whole Point, in spite of all these disturbances, is the comparative scarcity of weeds of introduction, which are noticeably fewer than in other parts of the Island. This is due to their failure, with one or two exceptions, to compete with the wild vegetation, which over great areas of the Point, consists of singularly close-knit, so-called 'closed' associations, and to the minute fraction of the Point now under cultivation, scarcely ten acres.

From what has preceded it would appear that the present vegetation of Montauk is to be viewed as exhibiting various stages in the development or perhaps replacement of forest covering as that is possible on the open downs, and in the face of environmental conditions to be considered later. The wind, the lack of moisture on the upper part of the downs, its presence close to the surface in many kettleholes,—all these play a part in determining the rapidity and the type of this process.

Several well marked types of vegetation are to be seen there now, and a description of these, with some notes on their probable position in the scheme will be given in the following account of "The Downs," "The Kettleholes," "The Hither Woods," and the "Region East of Great Pond."

These four have been selected because in them are to be found ecological problems, that are probably of more interest than anything else on Long Island. In them are well illustrated the all but world wide conflict of

grassland and forest. What the determining factors are behind that conflict will be dealt with, having in mind that much experimental work still remains to be done in unfolding the true story of the conflict. We may see and describe the results of it, hint, perhaps at the probable major factors of the struggle, but only by experimental work on the direct action of the wind, and some other environmental influences can we hope to come at a true explanation.

These do not necessarily comprise all the vegetation types to be found at Montauk, there are the ponds, for instance, or the salt marshes, and sand dunes. The latter, however, are not greatly different from similar places all over Long Island, and for that reason descriptions of them will not be repeated here.

THE VEGETATION TODAY.

THE DOWNS.

Some Englishman familiar with the Downs of Sussex and neighboring counties must have first applied the term to the rolling, apparently grass-covered, hills of Montauk. Except for the lack of chalk, the similarity to the South Downs is remarkable. Of course the plants in the English locality are different, but topographically, and so far as the general appearance of the vegetation is concerned the areas are quite similar, except that the Montauk Downs are all smaller and lower. The Downs in England are probably very primitive and, as suggested by A. G. Tansley, in "Types of British Vegetation," (pages 173 and 174) were never forested. He writes of the grassland association that, "It is unlikely that primitive man was responsible for the disforestation of such great areas of the chalk upland as are marked by traces of his existence, and the conclusion is therefore indicated that much of this grassland is primitive, or at least has existed since the conditions of climate resembled at all closely those at present obtaining."

It is scarcely credible that the Montauk Indians, with the crude implements which they were known to have had before the advent of the whites, could possibly have cleared such extensive areas as the English found covered by open Downs (approximately 6,000 acres), if most of it was primitively covered with woods.

And even if there had been some ancient cutting by the Indians, it may well be that at Montauk, as on the coast of Denmark, afforestation is impossible on certain specially exposed parts of the peninsula.

At the present time the dominant plant of the Downs is the grass *Schizachyrium scoparium*, which is of wide distribution over the greater part of the United States, and on Long Island is dominant mostly on these Downs, and on the Hempstead Plains. It is this plant that makes the generally grass-like covering of the Downs, and tinges with purplish-russet colors a landscape that is wonderful in September and October.

While *Schizachyrium scoparium* is dominant, there is associated with it a group of herbs that during different seasons, and because of their color, give definite character to the Downs: *Antennaria plantaginifolia* early in the season makes great areas of white cottony flower masses; in August and late July, myriads of *Polygala polygama*, with racemes of rose-purple

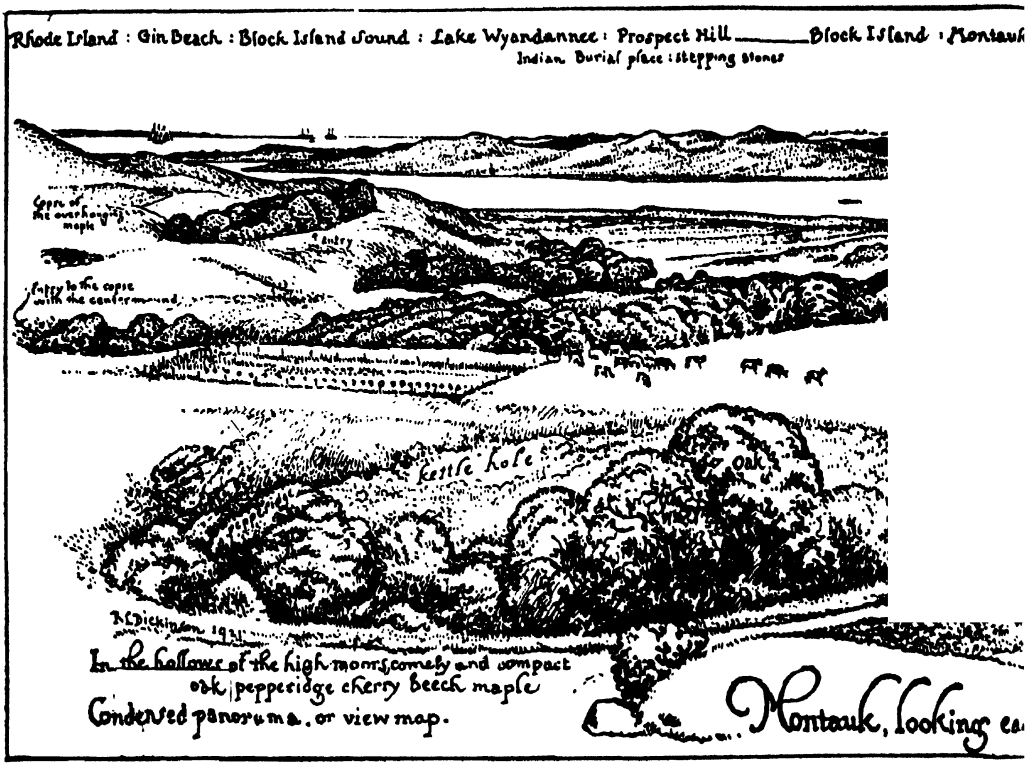
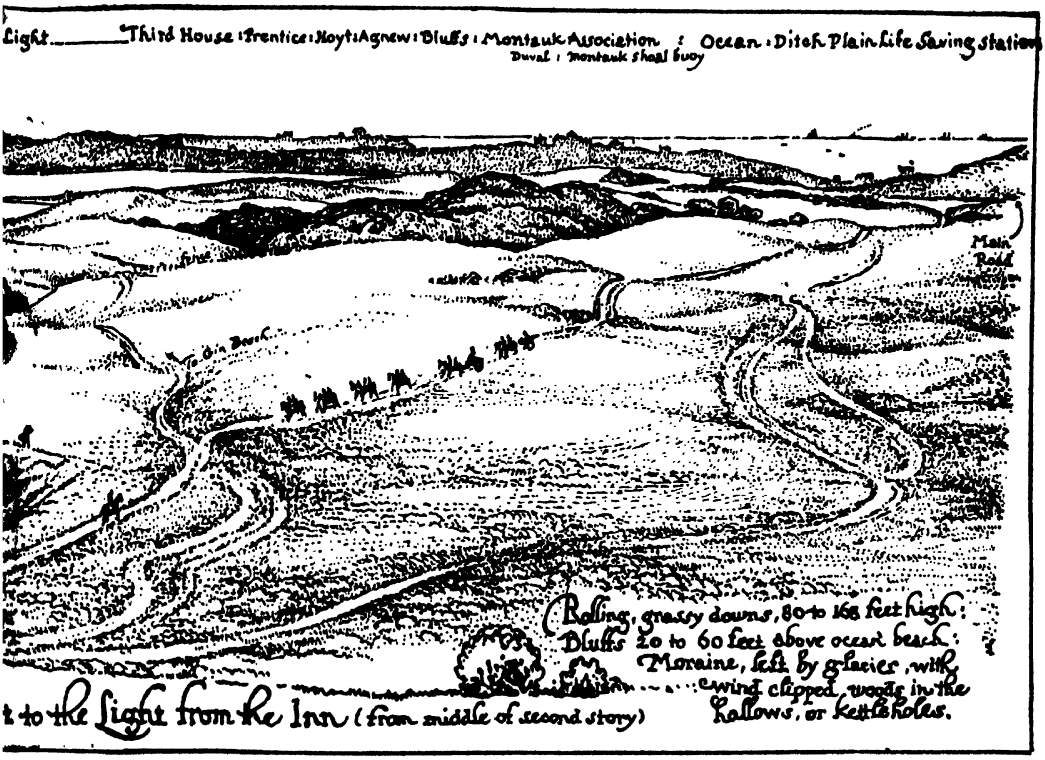


FIGURE 2. Panorama of Montauk. From pen and

(sometimes white) flowers give midsummer color to the hills, which are often splashed at the same time with scattered patches of the white-flowered *Sericocarpus asteroides*. A little later untold millions of *Agalinis acuta*, with small purple flowers, give a new note of color, followed by the violet-colored or often paler, *Ionactis linariifolius*, with its aster-like ray flowers. Pages of description could be written of this ever changing panorama of flowers over the Downs, to the possible exclusion of a detailed account of the composition of this vegetation.

Considering first the herbs, which make up nearly all the vegetative covering of the Downs, it appears possible to separate them into groups as to their frequency of occurrence. In the following list the dominant species comes first, followed in order of frequency, by those which, while still very common, are subsidiary:

Schizachyrium scoparium
Juncus Greenei
Deschampsia flexuosa
Sorghastrum nutans



nk sketch kindly contributed by Dr. R. L. Dickinson.

Polygala polygama
Sericocarpus asteroides
Antennaria plantaginifolia
Agalinis acuta

It is surely not without significance that these herbs are all perennials, able to endure the winter with some degree of certainty, and that all show some measure of protection against the wind. In the case of the grasses, and of *Juncus Greenei*, *Polygala polygama*, and *Agalinis acuta*, the leaves are so narrow as to offer little resistance to the wind; and partly in *Sericocarpus*, and wholly in *Antennaria plantaginifolia* the leaves are practically flat on the ground and offer no resistance at all.

These eight plants make up the great mass of the herbaceous vegetation of the Downs. By weight and mere bulk they far exceed all the rest of the herbs put together, for as will be shown presently, many other species found there are rare and some have only been seen a time or two. The fitness of these eight species for their particular role in the covering of the Downs is worth some consideration. Their adaptability to winds has already been

noted but some account of their distribution and habits of growth may throw light on their peculiarly effective place in the vegetation of these rolling hills.

The grasses *Schizachyrium*, *Deschampsia*, and *Sorghastrum*, mentioned above, and *Juncus Greenei*, are all plants that grow in close, dense tufts,

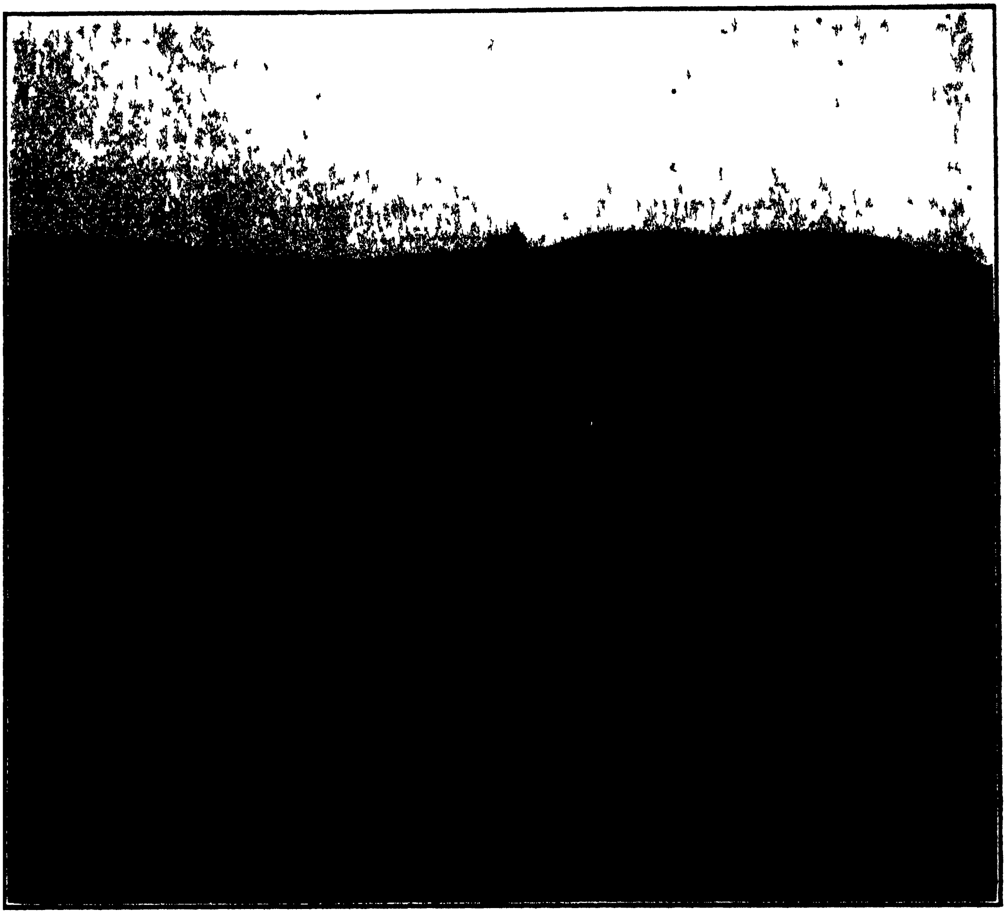


FIGURE 3. General view of the Downs at Montauk. The dark spots are mostly bayberry thickets (*Myrica carolinensis*). The dominant grass is *Schizachyrium scoparium*.

or clumps, and do not tend to make a true turf, of which, because of this habit, and the admixture of other species, there is practically none at Montauk. In a region so grass-like in character, the predominance of species that do not make real turf is somewhat curious. Perhaps of significance is the presence of the lichen, *Cladonia rangiferina*, which often carpets the Downs and through which all the species are apt to force

their way. All these grasses and *Juncus Greenei*, one of our only dry-land rushes, are plants of wide distribution outside of Long Island.

In the case of *Polygala polygama*, while it is of wide general distribution, locally it seems to be confined to the coastal region of Long Island and Staten Island. It is nowhere more common than at Montauk, where the usually uncommon white-flowered form is certainly not rare. Its great profusion among the grassland vegetation is perhaps due to its stiff wiry stem and foliage, so that it appears to be peculiarly unpalatable to cattle.

Sericocarpus asteroides, the tallest of all these primary species on the Downs, has also the broadest and most succulent leaves of all of them. So many are basal, however, and lie practically flat on the ground that they neither offer resistance to the wind, nor can they be nibbled by cattle. Perhaps the salvation of this white-flowered composite is its tough stem, only sparingly furnished with leaves, and its habit of nearly always growing isolated, not making such attractive grazing as the grasses, which, while they make no turf, are often found in dense clumps a foot or more in diameter. This plant is otherwise known through the eastern part of the United States.

Much the same is true of the survival of *Antennaria plantaginifolia*, with the additional fact of the soft white, almost velvety, covering of the leaves. This not only retards transpiration in a region where this is very rapid, but also protects the plant from cattle, who never seem to touch it. The plant is common throughout eastern North America.

While these eight species make up the mass of the herbaceous vegetation on the Downs, they are, of course, associated with many other plants, some of them common enough, others only scattered. These secondary species of herbs, arranged in the order of their frequency, are as indicated below:

Ionactis linariifolius
Agrostis alba
  Whether native in the north, or naturalized from Europe, this grass is at Montauk a relic of the great herds of cattle in the past. A good illustration of an introduced plant thoroughly mixed with the native vegetation.
Chrysopsis falcata
Crocanthemum canadense
Crocanthemum majus
Euthamia tenuifolia
Lechea villosa
Solidago nemoralis

Much reduced in size over plants from the central part of the Island.

Aster patens

Also *A. phlogifolius*, if that species, so far as Montauk specimens are concerned, be more than a mere form of *A. patens*.

Baptisia tinctoria

The tallest herb on the Downs, and very noticeable, as it is dotted all over the Point and every individual is made conspicuous by its stiff dome-like habit, instead of being merged in the general mass of the vegetation.

Carex Muhlenbergii

Chrysopsis mariana

Aster ericoides

Hieracium scabrum

Aster multiflorus

Often making exclusive patches, and rarely over six inches high, usually less. Its stunted wind-wrenched habit of growth is one of the most characteristic transformations of species at Montauk that are elsewhere taller and normally developed. Its dense masses of tiny white flowers, often flat on the ground, emphasize strikingly at flowering time, the reaction to the wind of this Aster.

Polygala viridescens

Potentilla canadensis

Also the form known as *P. pumila*.

Solidago rugosa

Much reduced in size over plants near the bottom of kettleholes, where the species is more abundant than on the Downs.

Viola fimbriatula

Kneiffia Allenii

A plant long thought to be endemic at Montauk, but now found elsewhere on Long Island. Its golden yellow flowers, low habit, and very general distribution over the Downs add a note of color in midsummer.

Galium pilosum

Cyperus filiculmis

Panicum columbianum

Achillea Millefolium

Another relic of man. A beautiful pink-flowered form is sometimes met with, particularly on the Downs just east of Great Pond.

Anaphalis margaritacea
Sarothra gentianoides
Panicum Scribnerianum
Hieracium marianum

While the foregoing lists of the primary and secondary herbs include, broadly speaking, the herbaceous vegetation of the Downs, other species are, of course, found there. These occasional specimens, erratic in their distribution, sometimes seen only once, add interest to the flora, without being of much importance in the development of it. A list of these species follows. All have been seen at least once, some are locally quite common. These are not arranged according to frequency of occurrence:

Sisyrinchium atlanticum and S. arenicola
Blephariglottis lacera
Ibidium gracile
Polygonella articulata
Potentilla monspeliensis
Lespedeza capitata
Cathartolinum striatum
Cathartolinum medium
Hudsonia tomentosa
Oenothera Oakesiana
Oenothera muricata
Bartonia virginica
Koellia incana
Koellia mutica
Trichostema dichotomum
Linaria canadensis
Plantago aristata; rather rare as an introduced plant.
Hieracium Gronovii
Eupatorium hyssopifolium
Eupatorium Torreyanum; also found near Culloden Point, but rare.
Solidago bicolor
Solidago juncea
Cirsium horridulum*

* This plant furnishes a good example of the possible changes in herbaceous vegetation of the Downs. Dr. Arthur Hollick who visited the region in 1890 wrote (Bull. Torrey Club **18**: 256. 1891) that "Some four years since [1886], so my driver informed me, a few plants of *Cnicus horridulus* made their appearance near the western edge of the hills. The prevailing winds scattered the seeds toward the east, until now [1890] it has complete possession over miles of what was formerly fine pasture land." Today nothing like such frequency is to be found.

Aster dumosus
Leptilon canadense
Erigeron pulchellus
Erechtites hieracifolia.

These, with the primary and secondary species, make an essentially complete list of the commoner herbs of the Downs. Other species could be included,* and more undoubtedly will be found, but for our general purpose of presenting as complete a picture of Montauk vegetation as possible, these will serve. So far as the Downs are concerned, *Baptisia tinctoria* is the tallest of these herbs and becomes therefore much more conspicuous than its actual frequency would suggest.† Practically all the other species, at least so far as their wind-swept habitat at Montauk has developed them, are low and hug the ground. Indeed so closely is this done, so perfectly does the open Downs' vegetation cover the hills, that, with the exception of these sentinel-like domes of *Baptisia tinctoria*, the hills of grassland look from a distance as though they were mown. Every undulation of the ground is shown and almost nowhere, as in so many of our landscapes, is the topography obscured by the vegetation.

The beauty of the Downs vegetation, so relatively limited as to species, and yèt so perfectly fitted to its environment, should not blind us to the fact that the region is within the general forest area of northeastern America, that forest cover is found in considerable quantity in the Hither Woods, the North Neck Woods, Point Woods, and in many of the kettle-holes. Whether or not these bare downs were once covered with forest, large areas of them today appear in a state of stable equilibrium. Woody vegetation on these wind-swept hills appears next to impossible, and yet there are evidences that some form of woody vegetation is making an attempt to cover at least part of what is now grassland.

There are to-day hundreds of tiny patches of "bush" scattered over the Downs, some only a foot or two in diameter, others covering, especially in

* One curious failure of a rather typically grassland plant to become established at Montauk is the case of the bird's foot violet (*Viola pedata*). This plant, which occurs in tremendous profusion on the Hempstead Plains, has never been recorded from Montauk.

† Mrs. Theodore Conklin, who has lived on the Point for many years told the writer (1920) that it is only since the Spanish American War in 1898, that *Baptisia tinctoria* has been found on the Downs. She relates that a few years after the soldiers left, the autumn and winter winds swept great quantities of the 'tumblers' against the side of "Third House," her home for many years. This was unknown before 1898. The case of *Cirsium horridulum* has already been mentioned, so that we have, within thirty years, two conspicuous plants that have [perhaps only temporarily] usurped these Downs, without changing the dominantly grassland character of the vegetation.

the lee, square rods in extent. To what chance of nature, or freak of the wind, to possible fires, or to the idle grazing of cattle, the origin of these tiny patches of bushes is to be attributed, no one can say. It is certainly true that they are more frequent and larger toward the bottoms of the kettleholes into which the Downs vegetation frequently penetrates, and in the lee. Their striking dark green foliage, against the purple and tan of the grassland, is obvious for a mile or two.

Before considering what role these patches of "bush" can play in the vegetation scheme of Montauk, let us record the species that make up these little islands of thicket in an ocean of grassland. Almost without exception, the major portion of these islands is made up of the Bayberry (*Myrica carolinensis*), very often associated with which will be *Rosa carolina*, and perhaps the whole mass bound together with *Rubus procumbens* (which often scrambles out into the grassland), or *Smilax glauca*. It is not without interest that both these binders make prickly forage, and that in nearly every one of hundreds of such patches of "bush" that were examined, one or both of these vines was to be found. Both the Rose and the Bayberry, under normal circumstances, would be several feet tall, here they are rarely more than a foot. There are scores of places where the wind keeps these flattened down so that while the patch of bushes may be many feet across, the shrubs will be only six inches high. Sometimes, but not very often, a slight undulation, a fortuitous boulder, with which the Point is strewn, or an effective lee will invite greater growth of these bushes. Such accidents seem always to be utilized to the full, and where they are operative enough, a species of Shad Bush (*Amelanchier intermedia*) will often get a foothold.

From this stage in the development of a patch, which may start with a single sprig of Bayberry, and end with a forlorn and stunted tree in the center of it, no one knows how long a time may have elapsed. Certainly in some of these patches such gnarled and stunted trees are to be found. They are never much over four feet tall, towards the tops of the Downs, and in many of the patches destroyed utterly by the wreaking of the wind. But the fact remains, that occasional trees do start in such patches, and that they certainly start nowhere else on the open Downs. The process is infinitely slow, the number of failures is large, and the number of patches of bush that seem the same, year after year, is rather striking evidence that even with the slight protection of Bayberry thickets, trees can hardly start and maintain themselves on the open Downs. Nevertheless, such protected spots, bleak though they appear to be, do sometimes nurture a young oak, or black cherry, or very rarely, a gray birch (*Betula populifolia*), and thus justify their existence as a stepping stone to something bigger, if not more picturesque.

Upon this conception, the Downs show infinite gradations between, as after temporary slides of sand and gravel, perfect nakedness and the attempt to produce some sort of woody vegetation. Because such a large part of Montauk Point is occupied by these open Downs, where available water is scarce, and the exposure to the winds is terrific, all expectation of a rapid development of forest is certainly hopeless. Where that one element, water, is added, as in the kettleholes, and there is protection from the wind, the change is abrupt and convincing. With almost perfect drainage, a little less than the average Long Island rainfall, but with twice the wind, with no shade, and even now a few cattle at large, the wonder is not that the Downs has developed a struggling tree here and there, but that it has not stayed permanently and exclusively grassland. At least some evidence from the plants points the other way, and as we shall see, there are other phases of the Montauk vegetation, beside the Downs, which seem to argue that vegetation, like the grassland, or the patches of "bush," or the kettleholes, is a complex organism that is born, develops, and ultimately reaches a climax of its career before death, or transition to something else. In such a scheme the Downs vegetation is in one of the earliest, and it may well be arrested, stages of development, where the grassland predominates, slightly more developed where patches of "bush" have started, still farther along where such patches have nurtured a small tree, which in the end, may form a nucleus for a new type of growth, made up of shrubs and trees, which is near the climax condition. It should not be overlooked that while the climax seems to be the forest, it is the youngest, because the most recently developed, of all the types of vegetation now found on the Downs, as the grassland is the oldest. Large areas of grassland have no *Myrica* in them, and in spite of a rainfall that should permit forest covering, may be edaphically incapable of producing it. Such areas, with apparently permanent grassland on them, are certainly examples of an arrested climax. Rainfall would normally permit forest cover, but wind velocity and insufficient retention of water on the slopes are inhibiting factors that are strong enough to stop, or make incredibly slow and difficult, the development of forest cover.

No account of the Downs would be complete without note of two interesting plants that have been introduced. The cloudberry or mountain bramble (*Rubus Chamaemorus*), at home in the Arctic, and on alpine summits of New England, was found between the Inn and Culloden Point on August 21, 1908, by Dr. William C. Braislin, who deposited specimens in the herbarium of the Museum in Brooklyn, since housed at the Brooklyn Botanic Garden. Diligent search has since failed to disclose this plant,

that at Montauk is hundreds of miles south of its true home. Migratory birds, known to make overnight flights from Labrador to Montauk, are supposed to be responsible for its introduction.

The other plant, probably introduced through human agency, is *Echinacea pallida*, found in 1914, and again in 1917, on the most exposed Downs, but by no means common. Its natural range is far to the westward on the plains of the middle west. Its rose-purple flowers nearly suggesting a single dahlia are very striking in their unfamiliarity at Montauk.

The Kettleholes.

The whole of Montauk Point is dotted with these depressions, some nearly a hundred feet deep, others mere swales, and the four largest covered with water, as discussed earlier. While the bottoms of none of the kettleholes, except, of course, the ponds, appear to be below sea-level, practically all the lowest of them has fresh water either near the surface, or, in the early part of the season, above it, forming a temporary pond, a few inches deep. The position of this water has a good deal to do with the vegetation, as will appear presently.

All of them agree in one particular, their sheltered seclusion from the wind in the bottom, often forming a welcome, if a warm haven for the summer tramper. The contrast between the bare wind-swept Downs and the bottoms of these kettleholes is tremendous. For details of the differences of the open Downs and the kettleholes, as sites for vegetation, see the section devoted to the wind in the chapter on "Factors of Control." So many of them are covered with trees and shrubs that casual visitors are inclined to think all of them are, which is actually far from the truth. Many are, some partially, others without a shrub or tree. While a general similarity in appearance seems to be true of those that contain woody vegetation, actually there are many variations, both in the species that occur in different kettleholes, and in the frequency of occurrence of those species that are common to all of them. Some of the deepest have considerable growth of the red maple or the sour gum, and in others that are not so moist, different species of oaks predominate.

If the forest is to be the ultimate covering of protected parts of Montauk, as it actually is now of Gardiner's Island, and, from historical records would appear to have been on at least some of the Point before disturbance by man, then those kettleholes that now have small editions of the forest in them are to be considered as more nearly approaching the climax condition than anything else on the Point. In other words, it should be possible to find gradations between kettleholes that have no trees or shrubs

to those that are full of them, and such early and late stages of development should be accompanied by at least some transitional stages.

A study of a good many of these kettleholes makes it seem probable that just these conditions are to be found today. Why some have been so delayed in their development as to show even at this late day

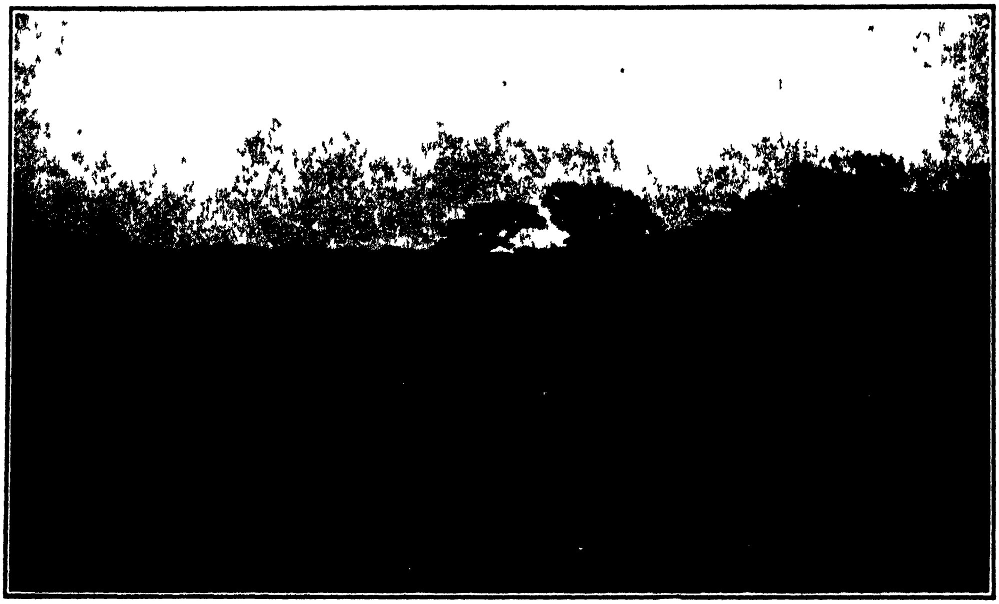


FIGURE 4. Pool in kettlehole near Culloden Point. Note amount of water and vegetation in it in September 1920, when this photograph was taken. In August, 1918, the water reached the edge of the kettlehole. See figure five for water-level in July, 1921. (Photograph by Barrington Moore.)

only the initial stages of it, is not very clear. In those where there is too much standing water, or where it does not recede early enough in the season, there is practically pond or pond-side vegetation that may be found over any part of Long Island. This is due to a too high and too steady water-table. Many other low kettleholes, however, have no standing water, and in practically all the cases where this has been observed the sides of the kettlehole (the Downs) come down very steeply, suggesting at once that material enough from these steep banks has filtered down to the bottom. This would not, of course, change the level of the water-table, but it would, and I think, has covered this over with silt a few inches deep in some cases and perhaps a few feet in the largest and most steep-sided of them. In contrast to this, the ponds that have been examined practically all have shallow banks, and it may well be that the presence or absence of standing

water is due to shallow or steep sides to the kettleholes. When it is remembered that no two kettleholes are topographically the same, few if any of similar depth, it is not surprising that a variety of conditions is to be found. There is, of course, one qualification to this statement regarding the presence of water in the kettleholes. Hundreds of shallow ones, too

FIGURE 5. Pen and ink sketch contributed by Dr. R. L. Dickinson of the same kettlehole as shown in figure four. Note condition of water on July 31, 1921, when the sketch was made and position of water in September, 1920. In August, 1918, the kettlehole was filled with water.

near the tops of the Downs to be near the general watertable of the Point, have no water near their bottoms, and most of these contain no trees but stunted ones such as are found among the patches of "bush" described with the Downs. Some, also, of these upland kettleholes, often mere depressions, have only characteristic grassland vegetation in them.

Whether or not this be the true explanation of the presence or absence of water in the kettleholes, the fact remains that all low ones are in one of three categories: open water, seasonal ponds that dry by midsummer, or a water-table that is below ground-level.

The purely seasonal nature of many of these kettleholes is well illustrated by one of them between the Inn and Culloden Point. On August 13, 1918, the bottom of the kettlehole was filled with water. In September, 1920, the same place had, as the accompanying photograph shows (Fig. 4), less than half as much water. On July 31, 1921, the water had reached the same level as in 1918, well shown by the sketch (Fig. 5) kindly made of the

place by Dr. R. L. Dickinson on that day. He shows the relative size of the body of water in 1918, by indicating the position of it in the center of the pool. Such changes cannot fail to affect the speed of establishment and the composition of the vegetation.

FIGURE 6. Open stage of kettlehole. Center with *Eleocharis obtusa.* The white-flowered plant toward the margin is *Eupatorium perfoliatum.* Note shore lines of seasonal fluctuations of water level.

In those where water is fugitive or lacking at the surface, the following is presented after a study of many kettleholes in all stages of development.

LOW KETTLEHOLES: OPEN STAGE.

Low kettleholes without woody vegetation are still occasionally to be seen, but in all those examined there was standing water a few inches deep in early June, but practical dryness by midsummer.

In such kettleholes there are usually well marked zones of vegetation dominated by some characteristic plant, or assemblage of them, and in the one illustrated (Figs. 6 and 7) all the lowest and therefore wettest part of it was covered by *Eleocharis obtusa.* This small sedge is succeeded, towards

its edge, by a fringe of vegetation made up of the following species, the dominant ones first, and the others in the order of their frequency:

Gratiola aurea
Hypericum boreale

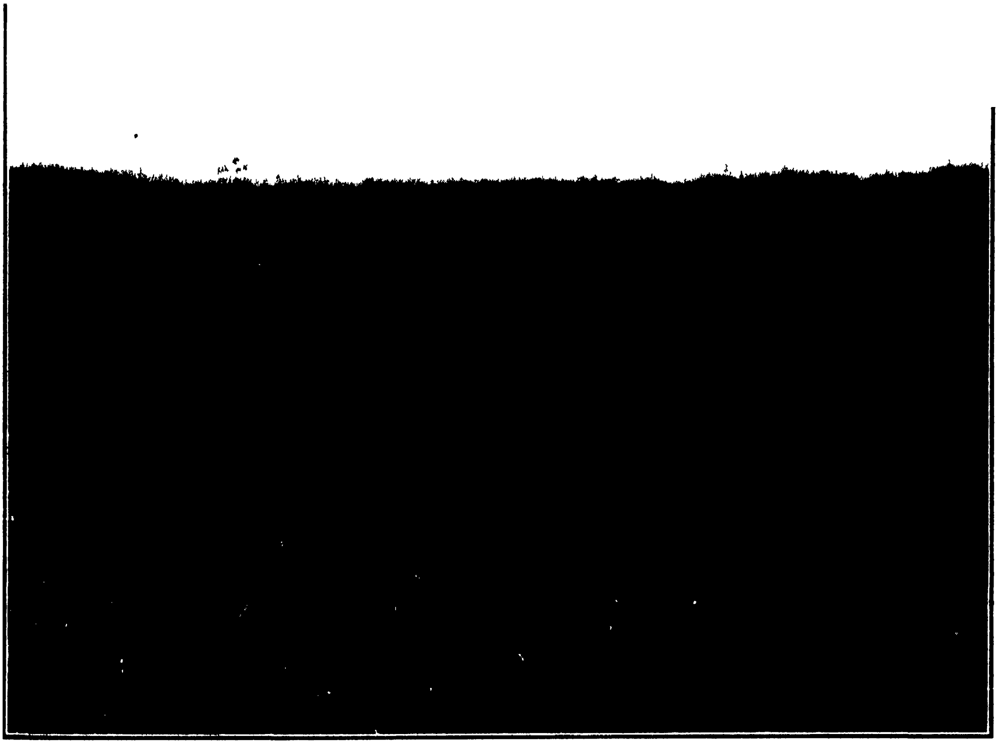


FIGURE 7. Details of marginal zone of vegetation in open stage of kettlehole. *Eupatorium perfoliatum*, *Steironema lanceolatum*, *Xyris flexuosa*, and *Gratiola aurea*, are among the commonest plants. Open Downs beyond.

Proserpinaca pectinata
A mud form as found in September, probably a submerged aquatic when water is present.
Viola lanceolata
Persicaria pennsylvanica
Echinochloa Crus-galli
A relic of grazing days? Native of Europe.
Cyperus dentatus
Scirpus debilis
Ilysanthes dubia
Juncus bufonius.

These ten species make up the bulk of the vegetation between the lowest part, occupied exclusively by *Eleocharis obtusa*, and the band of vegetation nearest the margin.

This marginal zone of vegetation occupies ground that, while well below the surrounding Downs, is high enough so that it is only covered by water for a short time in the spring. The plants here, therefore, do not suffer for water, nor are they smothered by it, as happens frequently in some kettleholes with uneven bottoms, or other conditions that permit too much standing water.

The vegetation of this marginal zone can best be shown by pointing out the dominant species toward the contact with the open Downs on the one hand, and toward the center of the kettlehole on the other, where it touches the zone for which the species have already been listed. In the following list of species the first and last are dominant nearest the inner and outer edges of the zone respectively. The others are arranged in order of frequency, reading from the top down for those nearest the inner edge of this marginal zone, and from the bottom up for those nearest the Downs. Toward the middle of the list are those species that are pretty commonly distributed all through this marginal zone.

Euthamia tenuifolia
  Dominant in that part of the marginal zone nearest the center of the kettlehole.
Steironema lanceolatum
  Often appearing dominant in midsummer from its wealth of conspicuous yellow flowers.
Gratiola aurea
Viola lanceolata
  Very often making large patches where it is locally dominant, but general and common through the lower part of the marginal zone.
Eleocharis tenuis
Rhexia virginica
Athyrium thelypteroides
Eupatorium perfoliatum
  One of the tallest herbs in the kettlehole.
Xyris flexuosa
Hypericum boreale
Juncus acuminatus
Stachys hyssopifolia
  Nearest the form known as *S. atlantica*

Ludwigia alternifolia
Cyperus dentatus
Scirpus debilis
Iris versicolor
Polygala cruciata
Lycopus americanus
Agrostis perennans
Glycine Apios
Oenothera muricata
Agalinis purpurea
Panicum virgatum
Dominant in that part of the marginal zone nearest the Downs.

These plants, with those already mentioned, make up, generally speaking, the vegetation of these low kettleholes that have no woody plants in them. The species in certain kettleholes differ somewhat, the individual frequency of the species even in the same kettlehole may differ in different years, but in dozens of them that are in this stage of development, the plants are mostly those indicated. One wide divergence from the type of a kettlehole in approximately this stage comes to mind not far from the Inn, where the bottom of the kettlehole is packed with *Decodon verticillatus* and *Hibiscus Moscheutos*, the Marshmallow, in about equal parts. Another, much nearer the Ditch Plain Coast Guard Station (see the map, Fig. 1) has exclusively *Hydrocotyle umbellata* in it.

In a few cases the first appearance of a woody plant is to be noted. In every case where only one shrub has been found it is invariably *Spiraea latifolia* or *Cephalanthus occidentalis*. These two bushes are certainly the pioneer ones at Montauk in populating kettleholes otherwise without woody vegetation. The appearance of either or both these bushes near the margin of a kettlehole does not, if, as often happens they are solitary or rare, change the general character of the place which is essentially a low, open kettlehole without woody vegetation. The appearance of woody plants in sufficient quantity to change, ever so slowly, the character of the kettlehole is an event of almost dramatic importance in the vegetation of the Point, and requires special mention.

LOW KETTLEHOLES: THE BEGINNINGS OF WOODY VEGETATION.

Many kettleholes at Montauk are in the condition just described, or are verging upon a still later stage in their development, when woody plants make a definite and apparently rather aggressive bid for occupancy.

Where this is pronounced the kettlehole may be found dotted with bushes, while in those just emerging from the purely herbaceous state, the few bushes found appear to be putting up a losing fight.

The permanent appearance of even a few bushes seems, in the kettleholes that have been examined, always to be associated with a lack of standing water, except perhaps in the early spring after the melting of snow. Whether the silting in of material from the banks is the true explanation of the disappearance of standing water or not, it is certainly true that in those kettleholes where water is fugitive or beneath the ground level, certain definite changes occur, followed by an encroachment of woody vegetation. The accompanying photograph shows a kettlehole in just this stage. A little water was found in it in June, none after. (See Figures 8 and 9.)

Its banks are very steep and the assumption that silted material has raised the floor of it enough so that shrubs will not smother from excess water, seems reasonable. It may also be that fires, which would scarcely affect herbaceous vegetation, would destroy pioneer shrubs in such places, thus greatly retarding the transition from an open kettlehole to a partially wooded one.

That there is always an orderly progression from open kettleholes to those about to be described, in which woody plants get a firm foothold, is probably not true. Some have been found where the process is arrested, due to unusually wet seasons or perhaps to fire, and one finds only dead shrubs, and a partial recrudescence of the purely herbaceous vegetation. But that this progression is going on, that bushes, and finally the dense wooded thickets of the climax type are ultimately developed, seems to be demonstrated.

The vegetation of a kettlehole of this developing type, where woody plants seem for the first time to have a firm foothold, is of interest, in view of the final stages to which it appears to point with rather definite directness.

As the photograph (Fig. 8) shows the center is dotted with dead clumps of *Scirpus cyperinus*, with here and there, in the higher places on the floor, a live one. Detailed studies of the remaining herbaceous vegetation in such kettleholes resulted in the following list of plants. The dominant species is given first, and in order of frequency, the others:

Triadenum virginicum
Gratiola aurea
Sium cicutaefolium
Lycopus rubellus
Onoclea sensibilis

Iris versicolor
Steironema lanceolatum
Juncus acuminatus
Scirpus cyperinus
Scirpus americanus
Persicaria hydropiperoides
Hundreds of tiny seedlings of this were also found creeping towards the center of the basin.
Eupatorium perfoliatum
Carex scoparia
Rhexia virginica
Ptilimnium capillaceum

There are sometimes other species found in kettleholes of this sort, especially large patches of *Aster novi-belgii* in some of its forms, but they are erratic and do not seem to occur with the regularity of those listed above.

A nearer photograph (Fig. 9) of the same kettlehole shows the arrangement and distribution of the shrubs among the assemblage of herbs mentioned just above. Towards the center of the kettlehole all the bushes are *Cephalanthus occidentalis*, whether dead or alive. As the photograph shows some are dead, due often to water smothering, which may sometimes occur in the center of the kettlehole even after bushes have gotten a foothold. Towards the edges of the kettlehole, and in addition to the dominant *Cephalanthus occidentalis*, four species of bushes entirely new to the kettleholes are found in considerable profusion. Of these *Rosa virginiana* is the commonest, *Rubus frondosus* next, and much more rarely *Vaccinium corymbosum*. Occasional plants of *Ilex verticillata* are found and, nearly on the edge of the Downs, *Spiraea latifolia*, which as we have seen is also found in kettleholes otherwise entirely without woody vegetation. These shrubs, and often *Eupatorium perfoliatum*, are often intertwined with *Convolvulus repens*, also a new plant in such developing kettleholes.

In a kettlehole southeast of the Inn toward the upper end of a deep gully that runs easterly from the road from the railway station to the site of the aviation camp (Great War 1917–1918), a curious variation of the encroachment of woody plants is to be found. The kettlehole is steep-sided and, in the early summer covered for at least a foot by water with a specific acidity of 30+. There is a marginal fringe of *Clethra* and *Ilex verticillata* neither of which is common, but the center of the kettlehole is full of *Cephalanthus occidentalis*. This is unquestionably a later stage in succession than those previously noted.

Kettleholes in this stage of development give an entirely different aspect to the landscape from those that have already been described, where low herbaceous plants predominate. The advent of shrubs, which is followed, of course, by trees, can be interpreted only as one more step in that process

FIGURE 8. General view of the beginnings of woody vegetation in low kettlehole. For details see text and Figure 9. In the foreground the dominant Downs grass *Schizachyrium scoparium* comes right down to the edge of the kettlehole. The white flower is *Eupatorium perfoliatum*.

of final woody covering going on very slowly, it is true, but none the less surely. The final stage or climax of the vegetation is found in the densely wooded, mysteriously dark and silent kettleholes, popularly supposed to be malaria-ridden, and into which few care to penetrate. These heavily wooded kettleholes are so much more conspicuous than the others that

have been noted that they attract more attention and are often assumed to be the characteristic condition of all kettleholes. The preceding account will have failed of its purpose if it is not now understood that these conspicuous wooded kettleholes are themselves the result of the development

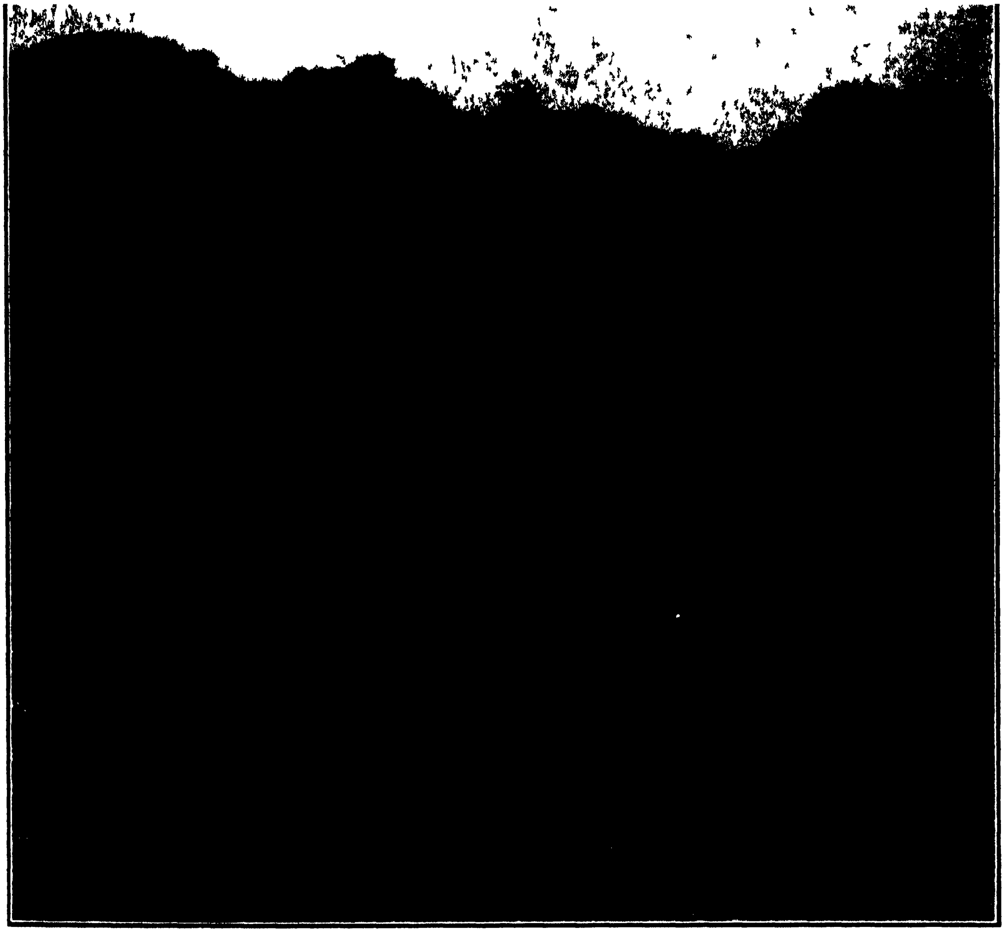


FIGURE 9. Details of figure eight Clumps of *Scirpus cyperinus*. The shrubs are mostly *Cephalanthus occidentalis*, and *Rosa virginiana*, more rarely *Vaccinium corymbosum* and *Spiraea latifolia*.

of the vegetation from the pioneer, and easily exterminated assemblages of plants found in kettleholes with long-standing or fugitive water, through a somewhat tentative woody stage to a climax of relatively permanent trees and shrubs with their associated herbs.

LOW WOODED KETTLEHOLES.

Dense masses of trees and shrubs, hopelessly tangled with Smilax, or Poison Ivy, or Virginia creeper,—this is the first impression one gets of the bottoms of most of the kettleholes at Montauk. Many of these are practically impenetrable without considerable cutting, and all of them are "cut off" by the wind. So universal is this action that many of the kettleholes appear to have their trees pruned or treated as a landscape architect might do for a definite effect. Trees and tall shrubs, such as the poison

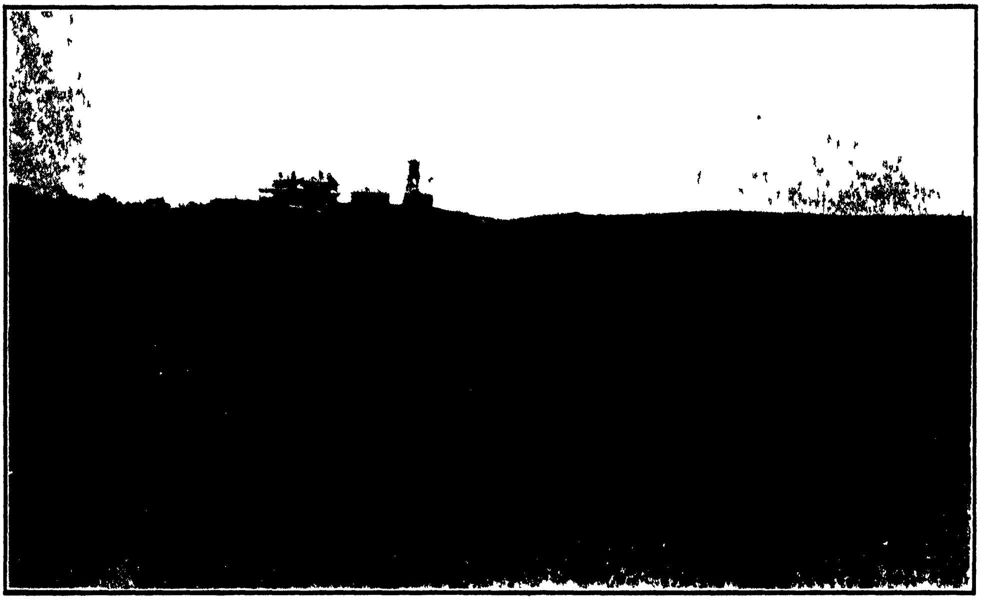


FIGURE 10. General view of wooded kettlehole at Montauk. (Photograph by Barrington Moore.)

sumac for instance, reach varying heights, depending on the depth of the kettlehole, which brings their tops just under the range of the wind that constantly sweeps above them. This often gives a wind-wrenched appearance to many trees, and very old specimens have a remarkably ancient and sturdy aspect, as though everything possible had been done to break through that impassable barrier, the depressing effect of which is so noticeable, and from which the depths of these wooded kettleholes provide the only real refuge.

Another feature of these wooded kettleholes that attracts attention is the sharp contact between them and the open Downs. The accompanying

photograph (Fig. 11) well illustrates this, which is characteristic of those wooded kettleholes that have consistent topography,—that is, where the moisture conditions are uniform enough to allow of practical similarity of woody vegetation, quite up to the edge of the Downs. In some, spurs of the kettlehole, with a higher level than the general floor, extend out into the surrounding Downs. In such cases the contact is obscured, and typical thicket vegetation replaces either type. This condition is not so common as the one illustrated which is characteristic of scores of the kettleholes at Montauk.

While the general aspect of these kettleholes is so uniform, and while, in the sequel, a list of their characteristic species will be given that is very generally typical many curious interlopers are to be found in some of them. If all the kettleholes at Montauk, probably some hundreds, could be studied as closely as the ones that have resulted in this account, there is little doubt that more species would be added to those known from the region. It is a commonplace, however, that the discovery of such would not in the least change the general aspect of the vegetation, nor the development of it to this climax. And it is because of this developmental phase of the vegetation, more than the discovery of a species new to the Point, that so much time has been spent in a description of it.

The characteristic species of these densely wooded kettleholes are given below. Under Trees, Shrubs, and Herbs, the dominant species is given first, and then the others, in order of their frequency:

Trees

Acer rubrum

The form more nearly approaching *A. carolinianum.*

Nyssa sylvatica

This and the red maple are dominant in practically all the low kettleholes.

Amelanchier intermedia

Frequently twenty feet tall and with trunk three inches in diameter.

Crataegus pruinosa

Fagus grandifolia

The last two are rare, and from the point of view of frequency, the first two are the significant species, as they dominate and give character to the kettlehole. Because of the depressing effect of the wind, the crowns of all these trees and the shrubs to be mentioned presently, are much congested and the canopy of foliage is thus so dense that it is almost dark in the interior. Some idea of the darkness may be realized by recording the

fact that in the heart of some of the largest of these wooded kettleholes there is no ground vegetation at all. This lack of herbs and their flowers merely accentuates the deep gloom of these dense stunted little forests. In the center of them one finds only the heavy canopy of foliage just overhead, and the dank carpet of dead leaves under foot. The accompanying

FIGURE 11. Sharp contact between edge of wooded kettlehole and open Downs. The flower on the Downs is the beautiful little purple-flowered gerardia (*Agalinis acuta*).

photograph (Fig. 12) gives some idea of the tangle of shrubs and trees in one of the wooded kettleholes viewed from the inside.

Shrubs

Amelanchier intermedia (bush form)

Aronia atropurpurea

Clethra alnifolia

Azalea viscosa
Viburnum venosum, and much less frequently *V. dentatum*
Sambucus canadensis
Rosa palustris
Vaccinium atrococcum
Ilex verticillata
Padus virginiana Mill. (Prunus serotina Ehrh.) as a shrub.
Toxicodendron vernix

These with the trees mentioned above, form next to impenetrable growths through which it is almost impossible to force one's way. It often happens that their branches are inextricably bound together by vines of *Smilax rotundifolia*, *Vitis aestivalis*, *Parthenocissus quinquefolia* and *Toxicodendron radicans*. The difficulty of getting through them, coupled with the almost funereal gloom of their interiors has made these wooded kettleholes an object of suspicion among some of the natives, and even among more sophisticated visitors.

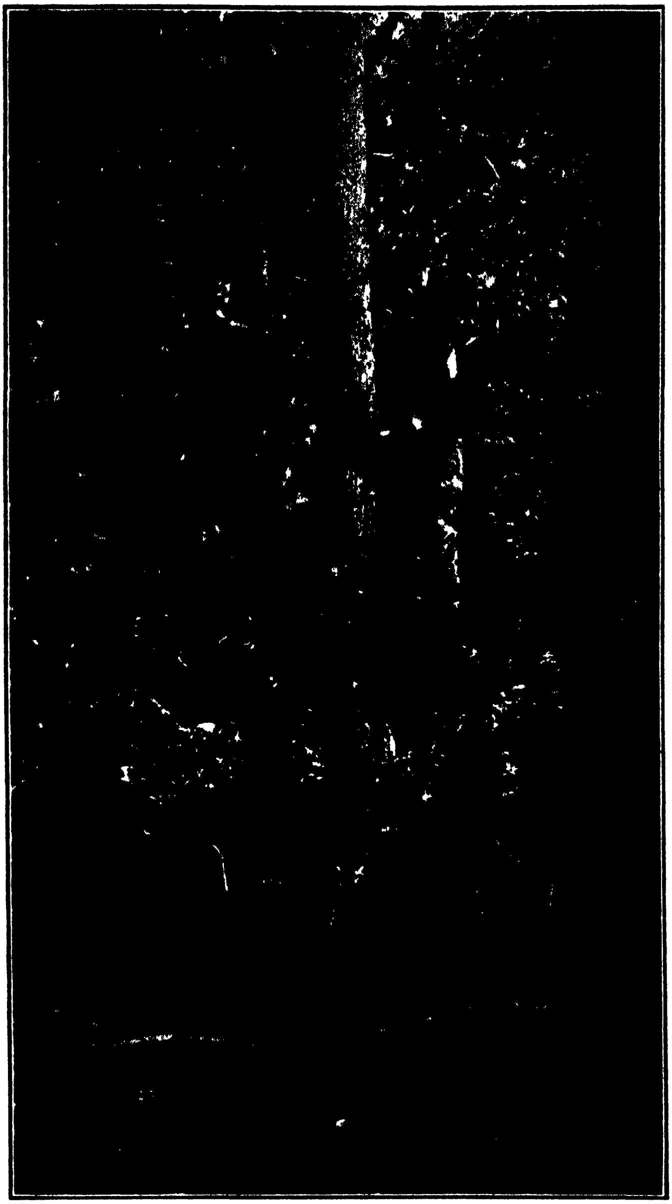


FIGURE 12. Interior view of wooded kettlehole. For details see text. (Photograph by Barrington Moore.)

Herbs

Toward the center, very often none.

Unifolium canadense
Uvularia sessilifolia
Osmunda claytoniana
Dryopteris noveboracensis
Boehmeria cylindrica
Iris versicolor (in deep shade)
Impatiens biflora
Eupatorium verbenaefolium
Galium Claytoni
Aster cordifolius
Arisaema triphyllum
Fragaria virginiana
Euthamia tenuifolia (toward edges)
Aster multiflorus
    Not at all like the form found on the Downs. These protected plants frequently 3 feet tall.
Viola cucullata
    Toward edge of kettle hole; rare
Solidago serotina
Aster novi-belgii
    In addition to the typical form others are found to which varietal names such as *elodes* and *atlanticus* have been applied.
Aster spectabilis (toward edges)

In many of these wooded kettleholes *Rubus hispidus* is very common as a ground cover and, except at the center, is very likely to run in and out among the stems of other plants, increasing the difficulty of walking. Dark moist places in these kettleholes are often carpeted for square yards by the beautiful feathery moss *Climacium americanum Kindbergii.* Of course, at the actual contact of the herbs of the kettlehole and the Downs there is nothing like such a sharp line as the photograph shows for the woody plants. There is often some encroachment of the Downs' herbs, in usually much changed form, into the kettlehole.

All wooded kettleholes are not of this type, as some with higher elevations have oaks predominating in them, but even in these the red maple and sour gum are often found toward the center. The shrubs and herbs are much the same in all wooded kettleholes, but the lists given by no means tell all the story, for occasional species are found in many kettleholes and nowhere else on the Point. *Ranunculus delphinifolius* is one for instance. The discovery of others is practically certain as the kettleholes vary a good deal in depth, in the configuration of the surrounding Downs, and in

exposure where there is a break in these, and in other particulars. The main fact of significance seems to be that the wooded kettleholes exhibit a climax condition of the vegetation, comparatively stable so far as changes are concerned, and in this respect unlike any of the vegetation types thus far dealt with. For we have seen that the most protected parts of the Downs may become invaded ultimately by patches of bush, which themselves sometimes lead to higher bushes and possibly, but rarely, to stunted trees. Where there is protection from wind this may result in considerable areas of scrub or forest. This has happened, notably toward Gin Beach, a region near the north (lee) end of Great Pond. Here there are considerable areas of stunted oak woods that appear to have started in the method suggested in the preceding paragraphs.

Most of the kettleholes at Montauk could probably be sorted into the different categories that have been described, or into easily recognizable variants of them. One or two curious exceptions are interesting, however.

In an upland kettlehole between the Inn and Culloden Point there is practically no Downs vegetation, but the floor of it is packed with *Triosteum perfoliatum*, interspersed with a thicket-like growth of *Euthamia tenuifolia*, *Solidago rugosa*, *Panicum clandestinum*, *Asclepias syriaca*, and an occasional bush of *Rosa carolina*. *Triosteum perfoliatum* besides this Montauk record is known only from a rich woods at Orient, then not for a hundred miles to the west and again in rich woods which is its usual habitat. Its occurrence in such profusion in this upland kettlehole, only just out of range of the wind, and in full sunlight, is curious.

The other kettehole is Great Pond, near the north end of which there is an island. This is just above the water level of the lake and contains the tallest trees at Montauk. In fact the appearance of this densely wooded island suggests an unbroken occupancy by the forest. The forest floor here is quite like that of other forests, and not at all like the undergrowth of the wooded kettleholes already described. Because of these conditions a list of the plants found there is given:

Quercus coccinea
Quercus alba
Quercus velutina
Quercus rubra
Hicoria sp.
Amelanchier sp.
Viburnum venosum
Corylus americana
Hamamelis virginiana

Cornus alternifolia
Sambucus canadensis
Benzoin aestivale
Parthenocissus quinquefolia
Vitis aestivalis
Toxicodendron radicans
Aralia nudicaulis
Pteridium aquilinum
Vagnera racemosa
Geranium maculatum
Syndesmon thalictroides
Phryma Leptostachya
Lysimachia quadrifolia
Scrophularia leporella
Solidago altissima
Solidago rugosa
Mariscus mariscoides
Pluchea camphorata
Hibiscus Moscheutos
Phragmites Phragmites
Typha angustifolia

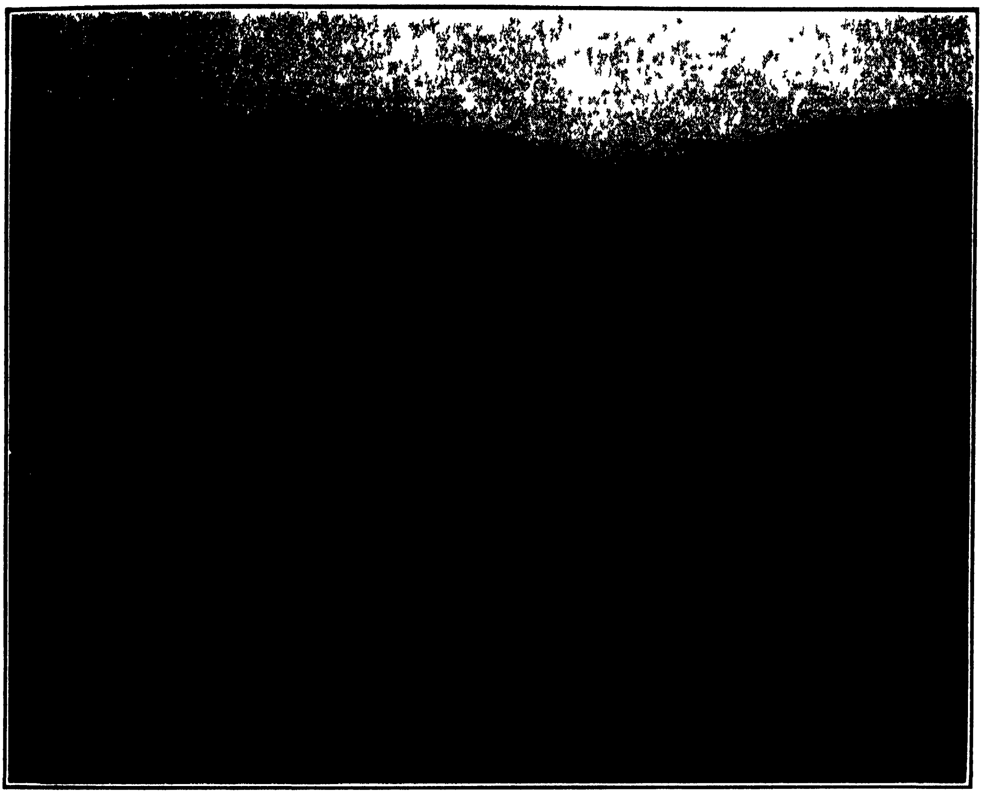


FIGURE 13. Lee contact of Hither Woods and open Downs. Note the vanguard of pioneer oaks creeping out from the edge of the forest, and, for comparison, the abrupt edge of the ordinary wooded kettleholes (Fig. 11).

THE HITHER WOODS.

If other evidence as to the gradual afforestation of some parts of Montauk were lacking there would still remain the Hither Woods, and its eastern or lee contact with the Downs, to confirm the point. Nowhere else on Long Island is there such a splendid illustration of the encroachment of a forest over the grassland as at the northeasterly contact between these woods and the Downs, about a mile west of the village.

The Hither Woods, predominantly oak, present an extraordinary appearance when compared with other forests on Long Island. The woods extend for about four miles west of Montauk and they are dense. Apparently they have always existed, since the earliest record of the first settlers at Easthampton speaks of them. J. A. Ayres who visited the

region in 1849 wrote then of woods at Montauk, as follows: "There are two tracts of woodland, known as "the Hither Woods," and "the Point Woods." Solitary and decaying trunks over all the country show that not many years since it was covered much more extensively and perhaps wholly with forest."

There is all the appearance today of great age for certainly the trees look very old. Many times they are not over forty feet tall, so that it is not their height that suggests age. Festooned as many of them are by lichens, and the forest floor under them often carpeted with *Cladonia furcata racemosa*, they stand "like the druids of eld," clad in the misty grayness of antiquity. The frequency of trees that have toppled over as they died, and lie rotting on the leaf-carpeted ground—all these, with the undisturbed look of the place, give one just such an impression of long occupancy for this forest, as the historical records indicate.

While the woods are thus a striking feature of the landscape, it is their lee contact with the open Downs that is of chief interest in considering what is the role of this forest in the vegetation history of the Point. So that we can better understand the composition of this forest, and as a record of what sort of growth it is that seems to have such an aggressive fringe, the following list is submitted. The species are arranged under Trees, Shrubs, and Herbs, and under each of these groups the species are listed in the order of their frequency.

Canopy trees
- Quercus velutina
- Quercus alba
- Quercus coccinea
- Quercus rubra (rare)

Undergrowth
- Kalmia latifolia } dominant
- Gaylussacia baccata } dominant
- Sassafras Sassafras rare, only young plants seen
- Padus virginiana
- Vaccinium angustifolium
- Ilex opaca
- Amelanchier canadensis
- Amelanchier nantucketensis
- Parthenocissus quinquefolia
- Smilax rotundifolia
- Vaccinium vacillans, frequently with *V. angustifolium* making large exclusive patches

Undergrowth
Herbs
Aralia nudicaulis
Epigaea repens
Melampyrum lineare
Trichostema dichotomum
Chrysopsis mariana
Aster patens

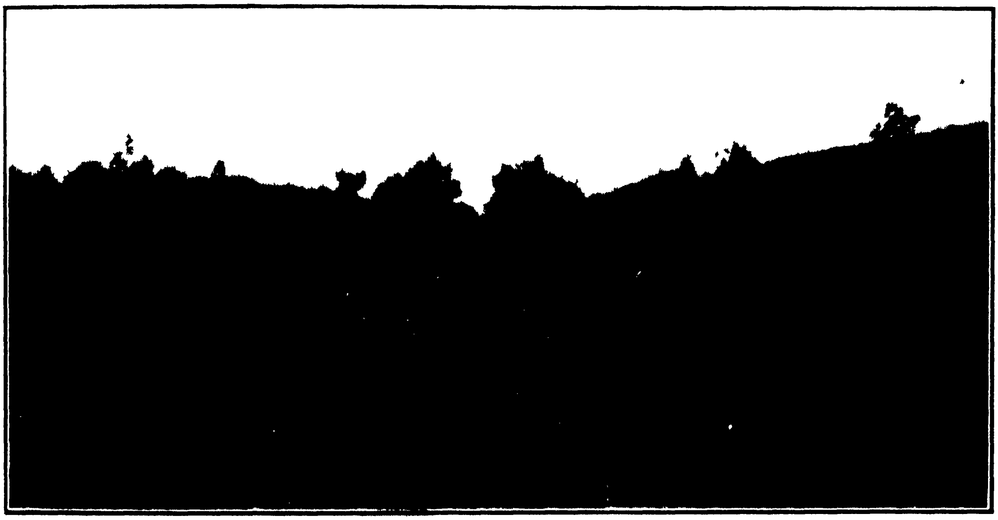


FIGURE 14. Pioneer oaks going out over the Downs from the lee side of Hither Woods.

Solidago bicolor
Carex pennsylvanica
Danthonia spicata, mostly in openings
Crocanthemum canadense
Crocanthemum dumosum

The foregoing gives a fairly complete idea of the composition of the Hither Woods near the edge of it, and the same general condition is found some mile or more west of the contact. Quite unlike the contact between the low wooded kettleholes and the Downs, which is very sharp, the Hither Woods–Open Downs contact on the eastern edge is by no means so, as our illustrations show (Figs. 14 and 15). There is in fact so much penetration of the Downs by these pioneer woody plants that just at this point there seems unfolding before us a bitter struggle for supremacy between these different types of vegetation, and the grassland is putting up the losing

fight. The evidence of this contest for new land, as it comes to that in the case of the trees, seems clear enough and to illustrate it, a section extending from pure grassland (east) to pure forest (west) has been studied in considerable detail. Because topography is such a vital factor in supplying shelter from the wind a rough cross-section of the hill is given to show the conditions at the point the section was taken.

Beginning at A (Fig. 15) the top of the bare Down, there is much the same condition as that noted under the general description of the Downs,

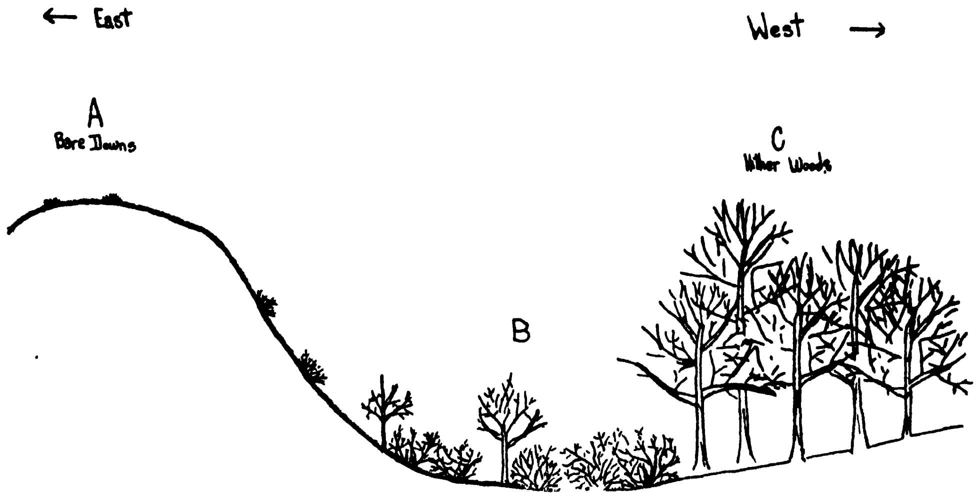


FIGURE 15. Diagrammatic section from the Hither Woods (west) to the bare open Downs (east), about 1 mile west of Montauk Village. The hill at A is about 50 feet high.

A. Bare Downs, with herbs and scattered clumps of stunted bushes.

B. Tension zone with occasional Oaks and much greater profusion of shrubs which are taller than at A.

C Edge of Oak forest at the Hither Woods For associated shrubs and herbs under these trees see text.

but with this difference. Here there are more numerous and larger patches of stunted bushes, and these are not of the species there described. Two of these new shrubs are interesting as being common bushes and of normal height a short distance away in the protection of the Hither Woods. At A, however, both *Comptonia peregrina* and *Gaylussacia baccata* are not over eight inches high, and frequently they make patches 30–50 feet across. That these and *Amelanchier canadensis* have "escaped" from the Hither Woods onto these open Downs, seems a conclusion almost axiomatic. All of them, and other woodland species, to be noted presently, have been found on the Downs only at this contact with the Hither Woods.

These three shrubs, with their associated plants, serve as pioneers for the serious invasion of the grassland by the forest. On the top-most part of the Downs these three shrubs are found only in rare patches. But as one goes down the hill toward B they increase in size and frequency tremendously, merging finally at C with their more usual prototypes that occur in and along the edge of the Hither Woods.

The interlacing of these two elements along this contact makes one of the most interesting features of the vegetation of Montauk. On the top of the hill, A, are mostly bare Downs with quite typical Downs species. Then as one gets closer to the woods there is the progressive disappearance of true Downs species, the flourishing of "escapes" or pioneers from the woods, overtowered presently by the vanguard of the oaks, for which, in a sense, they have been preparing the way. It is, of course, not such a simple matter as the ease of description might indicate. Many local irregularities, such as breaks in the Downs, exposure to the winds and so forth may arrest this process or modify it. In fact along certain places, where the Hither Woods is close to and exposed directly to the sea winds these stragglers from it out into the Downs are practically unknown, as we shall see presently. But where there is even slight shelter there is always the condition that has been noted.

At and near B (Fig. 15) where the struggle between the Downs' plants and the pioneers from the woods is most intense the following plants were found, arranged in order of frequency. Those that are of the Downs contingent are in *italics*, while the Hither Woods element is printed in bold face type. A few plants of general distribution over Montauk, or of no special significance in the struggle for occupancy are in ordinary type.

Gaylussacia baccata
Rubus flagellaris
Comptonia peregrina
Agrostis alba
Deschampsia flexuosa
Rhus copallina
Asclepias amplexicaulis
Schizachyrium scoparium
Padus virginiana
Amelanchier nantucketensis
Aster patens
Euthamia tenuifolia
Chamaecrista fasciculata
Rosa palustris

Anaphalis margaritacea
Chrysopsis falcata
Crocanthemum majus
Moehringia lateriflora
Myosotis virginica

In certain places at the bottom of this slope there are large, practically exclusive, growths of *Comptonia peregrina*. Over a considerable part of this area there is an impenetrable tangle of *Rubus procumbens* scarcely over three inches tall and a conspicuous inhabitant of the patches of bush over the rest of the Downs.

FIGURE 16. Open grown specimen of black oak (*Quercus velutina*) at the edge of Hither Woods, three feet in diameter at breast height. (Photograph by Barrington Moore.)

Among the miscellaneous growth, made up of elements from the Downs and the woods, and both actively attempting to appropriate the ground, there is evidence that the pioneers from the woods are winning. The most convincing features of this aggressiveness of the woods' plants are the numerous oaks which push out from the woods and find at least sufficient congeniality to persist in this tension area. Everywhere where the conditions produced by pioneer plants from the woods have made the escape of these oaks possible, they are sure to be found. This aggressive expansion must end in a considerable curtailment of the Downs area ultimately.

The oaks reach really exposed places toward the tops of the Downs only rarely, and with apparently great difficulty. But as in many other things, nothing succeeds like success, and once the start is made, it seems only a matter of time, due to increasing protection from the wind as the growth becomes gradually thicker, when the open Downs itself will be inundated by this ever encroaching woody invasion, infinitely slow as time goes, but from all the evidence available, as certain as the tides. Just how fast this is going on only a study over a series of years would show. But it does seem as though this contact between the Hither Woods and the Downs was perhaps the most energetic of all the different types of vegetation that seem to have as their common goal the afforestation of parts of the Montauk Peninsula, if that is climatically and edaphically possible.

There are some hints as to the rate of this encroachment of woods over grassland. About 400 feet west of the present contact with the open Downs, and in the midst of the dense shade of surrounding oaks is a dead *Juniperus virginiana*, which appears to have died within the last ten years. Increment borings show it to be at least eighty years old when it died, and adding ten years since death gives us about 90 years since it was a seedling.

This could hardly have started in the shade of the forest, and would, if it followed ordinary procedure, have started out in the open, or more likely still, in the area that then corresponded to the present fringe of the forest. Since that time the forest has gone out over the Downs about four hundred feet, submerging and ultimately killing the cedar. In other words, the evidence from this dead cedar would indicate a rate of forest movement of 400 feet in about 100 years.

Atthe present contact, but quite out in the open, and perhaps 100 feet from the forest edge, there are scattered young oaks, as shown in the photograph (Fig. 14). One, a *Q. velutina*, 14 feet tall, 6 inches in diameter, proved by core extraction to be 15 years old. By no means all the area between it and the edge of the woods, is yet occupied by pioneers from the forest, so that in the 15 years since it started there has not been any great speeding up of the process.

There is also other evidence, from the oaks themselves, that the Hither Woods have not always been as extensive as they now are. Many trees, particularly near the margin of the woods, show unmistakable evidence of having, in their young stages at least, developed in the open. The accompanying illustration (Fig. 16) shows a branching system that no forest grown specimen of oak could have produced. We could, from this evidence alone, say that most certainly the Hither Woods are spreading wherever possible, and that the branching of nearly all the oaks that have been

observed near the edges of the woods confirms the point. True forest-grown specimens of oaks are found only toward the center of the woods or in hollows.

The evidence along the eastern edge of the Hither Woods that they are gradually spreading still more eastward seems conclusive to the writer,

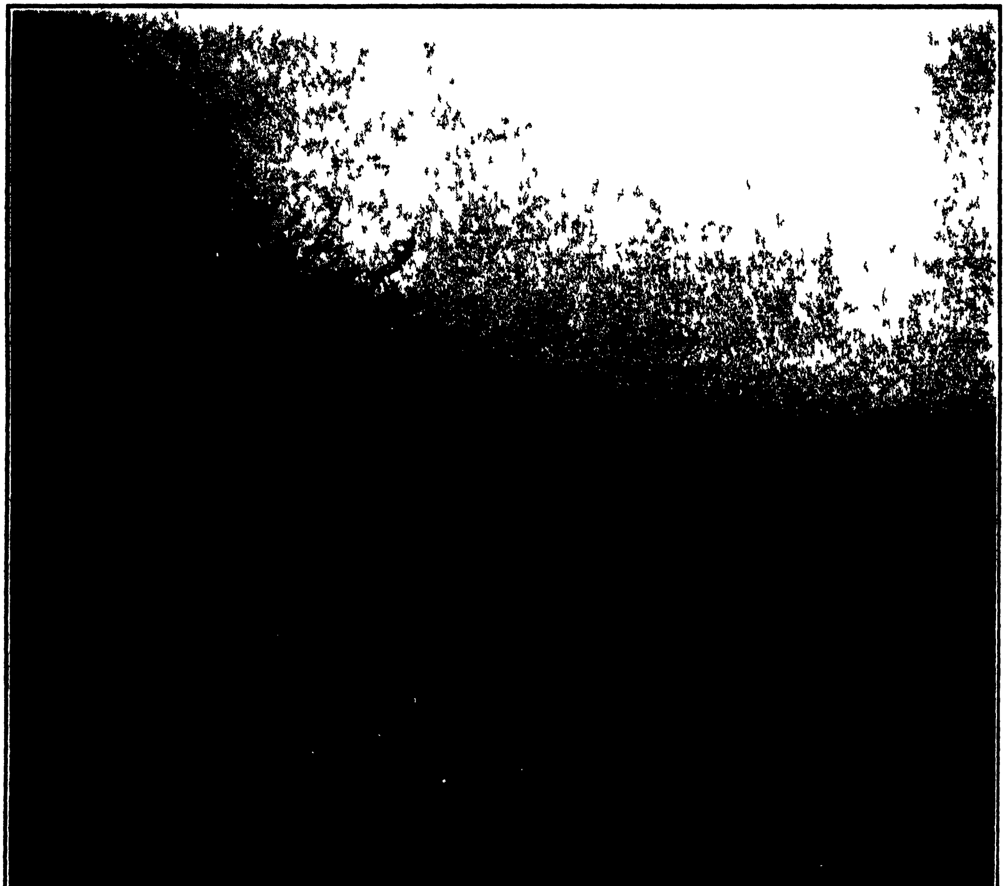


FIGURE 17. Wind clipping at the edge of the oak forest on the windward side of Hither Woods. Photo January, 1923.

and the explanation also appears to be indicated that this encroachment over the grassland can be accomplished only to leeward, which means generally to the eastward. Perhaps the best illustration of this wind control of the invasion of grassland by woods is furnished by the south side of the Hither Woods at Montauk. Facing the sea, they are subject to the violent southwest winds of summer, and the forest wall is abrupt (Fig. 17). No

vanguard of pioneers spreads out over the grassland for on these exposed Downs no pioneer can stand up.

Whether the violence of this wind is actually reducing the size of the forest only marked plots studied over a series of years would prove. The present site, and probably the general extent of the Hither Woods has existed from very early days, as David Gardiner, in his "Chronicles of the Town of Easthampton" writes of the early condition of the country thus: "To the east of this [Napeague] was Montauk, a high and hilly region of rich land, where resided the tribe of that name, over whom Wyandanch exercised control. Along the whole sea coast of the town, the border of the upland produced a scrub oak, but the trees being gradually protected by each other, from the violence of the winds which reached from over the wide spread ocean, enlarged in height and size as they receeded. The oaks were the predominant tree; they were of large growth, and, in the openings, of very extended branches."

There are, however, numerous historical references to the diminution of these woods, none of which are of any real value, as none that has been seen are for marked plots. It is certainly true at the present time, that on this southern side, there is no attempt worth mentioning of the forest to creep out over the Downs, such as we have seen it do on the more or less protected east side.

About half way from their western end, not over half a mile from the beach, the contact is very abrupt. The woods at this point consist of *Quercus alba* and *Q. coccinea* dominant, with a small mixture of *Padus virginiana*, *Hicora sp.*, and a few shrubs such as *Rubus nigrobaccus*, *Rhus copallina*, *Rosa virginiana*, and *Gaylussacia baccata*, tied together with Virginia Creeper, *Smilax glauca* and *S. rotundifolia*.

The herbs and other undergrowth under this forest, which is about one-half the usual height, although obviously mature as evidenced by the old trees that fall naturally, are the following, arranged in order of frequency.

Lysimachia quadrifolia
Rubus hispidus
Deschampsia flexuosa
Solidago rugosa
Aster ericoides
Nabalus trifoliolatus
Acalypha virginica

Just beyond are the open Downs with vegetation typical of such places. In them only a rare white oak seedling is to be found, usually not over a foot high, its few leaves browned and wind-scorched. Stragglers from the forest such as *Gaylussacia baccata* and *Rubus nigrobaccus*, mixed with such

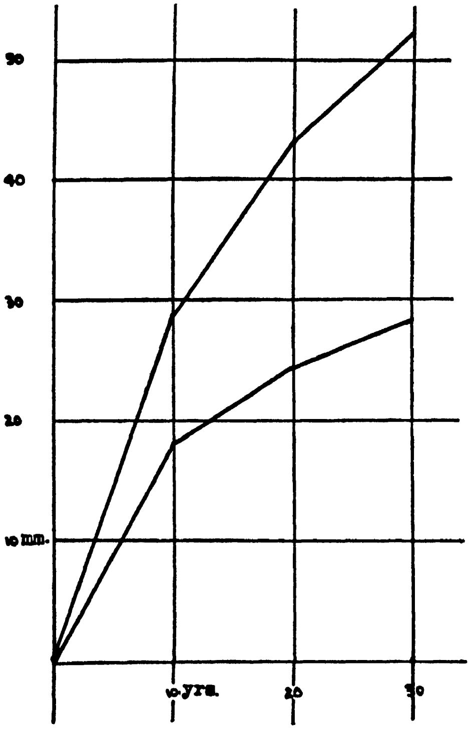


FIGURE 18. Rate of growth of the scarlet oak (*Quercus coccinea*) on the windward and leeward sides of the Hither Woods, expressed in increase in mm. of diameter at each ten year period. The hardness of the wood prevented deeper increment borings than are indicated. Upper curve an average of 20 trees on the leeward side; lower, of 20 on the windward side.

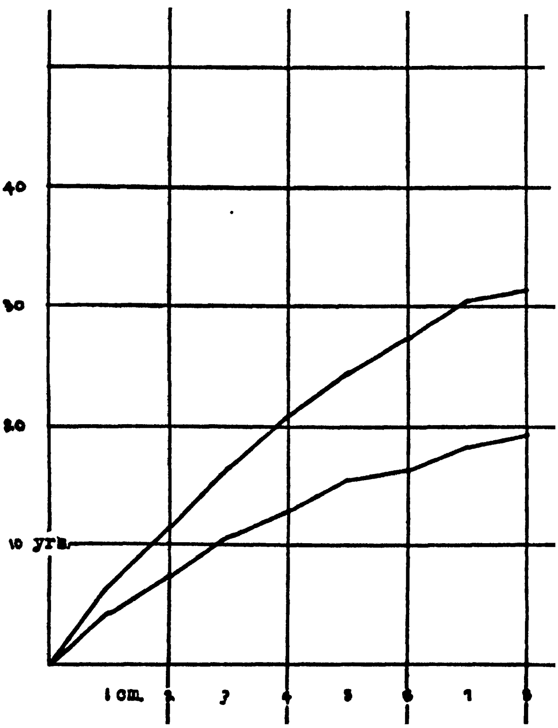


FIGURE 19. Age in years at each cm. of diameter growth of the scarlet oak (*Quercus coccinea*) on the windward and leeward sides of the Hither Woods. Upper curve = wind ward side, lower curve = leeward side.

typical Downs shrubs as *Myrica carolinensis* make small patches of "bush," but conditions for invasion by trees, are so much more severe than at the east end, that they present a practically impassable barrier to forest encroachment on this windward face.

In attempting to get more direct evidence of the effect of the wind on the growth of the scarlet oak on the windward and leeward sides of the Hither Woods, borings in many trunks were made. The cores so extracted in each case came from trees about twelve inches in diameter. Those taken from trees on the windward side of the woods were all taken in the direction of the wind, to overcome any irregularity, by averaging, that might result from the effects of the wind on eccentricity.

On the leeward side of the forest the trees average 28.8 mm. diameter growth in the last ten years, as against 18.4 mm. during the same decade on the windward slope. For the ten years previous to this the scarlet oak averaged 43.1 mm. in the lee and only 24.3 mm. where exposed.

To put the case in another way, it took the trees in the lee and those exposed to the wind very different periods in which to develop similar girths, if, indeed the exposed trunks will ever catch up with their better protected brethren. The accompanying charts (Figs. 18 and 19) show their growth curves and relative rate of growth graphically.

The Region East of Great Pond ("The Point Woods")

As we have seen, the wind seems to be the chief factor in checking the spread of woody plants, first in the open Downs, where the patches of bush are at first small and weak, then in the kettleholes, where, if they are not low enough to be within reach of water and at the same time out of reach of the wind, their woody vegetation is sparse; and lastly, along the edge of the Hither Woods where initial attempts of the trees to really capture outlying bare Downs are stopped or retarded by the wind. It might readily be supposed that if there were a place at Montauk where protection from wind was perfect, or at least greater than elsewhere on the Point, this should exhibit quite other types of vegetation than those already described. That there is such a place and that it does have an entirely different aspect from anything else at Montauk will be sufficiently clear from the following.

From Prospect Hill to the Point there is a long stretch of country which, at least to the south, is more or less in the lee, so far as west and southwest winds are concerned. All along the sea from just east of Ditch Plain to the

Lighthouse there are high bluffs rising from the sea sometimes as much as 75–100 feet, which is a considerable height for Montauk. There is thus a large area more or less in the lee stretching from east of Prospect Hill to the Lighthouse and from just back of the coastal bluffs more than half way to the shore of Gardiner's Bay. Not all of this area is covered with shrubs and trees, but the better part of it is. So dense is the growth in many places that it is practically impenetrable. Trees up to thirty feet are common enough in the lower parts of this region and only on the very top of some of the highest Downs is the expected grassland vegetation found. The density of the growth, diversity of the species found there is immediately noticeable to the casual traveler, after he leaves Great Pond to go toward the Lighthouse. Where before one has been traveling over little more than easily diverted trails over the grassland, from where the woods begin to the Lighthouse, the road winds in and out among hills, it is true, but here they are mostly covered with a dense growth of woody plants. No very careful study has been made of this region, the largest in area and probably the richest in species of plants at Montauk. One reason for this is the difficulty of getting about, and the other is that here the process of forestation is so far along that there is not the interest as in other parts of Montauk, where, as it were, things are in the making, rather than as at this place, they are very nearly made over. It is only because of the wind, which, while considerably reduced in its action, is by no means impotent, that this woody growth at Montauk Point is not higher. It may well be ultimately as high as the forest on Gardiner's Island, and before the great storm of 23 September, 1815, it was said to be so. (See the section on climate in "Factors of Control.")

As a record of what has been observed in these woods at Montauk Point, which as here defined means the region from Prospect Hill and the cottages east of Ditch Plain to the Lighthouse, the plants peculiar to or characteristic of the Point have been so designated in the list of plants of Montauk, which is the final section of this sketch.

No mere list of species, however, would convey an idea of the heavy growth of shrubs and trees in this region of Montauk. The trees are mostly as large as at Hither Woods, but the diversity of environment, for there are several ponds, bogs, and swamps, is such that the number of different species is greater than all other parts of Montauk combined. In the boggy places, about the end of May this part of the peninsula is aflame with *Arethusa bulbosa*, in fact it is more common here than elsewhere within the observation of the writer.* It is here too that *Kneiffia Allenii*, a plant

* Mr. Edward S. Miller, who with H. W. Young, wrote a "Catalog of the Plants of Suffolk County," in 1874, and who lives at Wading River, reports that *Arethusa* is probably more common in the bogs north of Manorville, than anywhere else on Long Island.

long thought to be endemic at Montauk is most common. *Viburnum venosum*, a rare shrub, is also found here in the thickets and is by no means scarce. In these woods too are found the common columbine, *Aquilegia canadensis*, so common in the rocky places in the region north of New York, but on Long Island exceedingly rare at a few other places on the north shore.

Within this region too is the finest growth of the Mountain Laurel known to occur on Long Island. Plants up to 20 feet, with stems three inches in diameter are to be found by diligent search, an exact locality for which prudence would not advocate divulging.

Perhaps the culmination of what the vegetation of Montauk will do, if partly protected from the wind and given adequate water supply, is to be found near the center of these woods. Here one may find as nearly typical a Beech-Maple climax forest as can be found anywhere else on eastern Long Island, except at Gardiner's Island. Neither at Montauk, nor, elsewhere on Long Island, is there a true representative of the Beech-Birch-Maple forest type, so common over great areas northward.

None of the trees is over forty feet tall, however. Mixed with the beech and *Acer rubrum* are scattered *Nyssa*, *Quercus rubra*, *Quercus alba*, *Hicoria glabra*, *Ilex opaca*, and *Hamamelis virginiana;* the last two the largest of any specimens seen on Long Island, nearly thirty-five feet high. The Witch-hazel here has a maximum girth of twenty-one inches.

Through these trees meanders a sluggish stream flowing towards the north, its shaded waters crammed with *Vallisneria spiralis* intermixed with *Fontinalis Novae-angliae*. Along the shallowest of its banks are zones of *Arisaema triphyllum* or *Spathyema foetida*, among which, or on somewhat higher sites are masses of *Viola pallens*, *Viola cucullata*, and *Thalictrum revolutum*. Other herbs scattered through the lowest part of these woods are *Osmunda cinnamcmea* and *Athyrium Filix-foemina*, which are rare, and *Vagnera racemosa*. Somewhat above this lowest level, there is a zone of herbaceous vegetation almost completely dominated by *Anemone quinquefolia* and, scarcely less so by *Trientalis borealis*. Almost no shrubs are found at this point, only *Benzoin* and *Sambucus canadensis*, surviving the dense shade of these woods.

All along the north side of these woods the region is very nearly typical Downs, such as that described earlier in this account. One difference, however, is that in this region near the Point there is so much low land and the substratum is sufficiently acid, that cranberries are more plentiful than in almost any other part of Long Island. This has been true for over a hundred years as the following, from the town records of Easthampton of

April 7, 1789, shows: "Voted and agreed on by major vote, on the day above-said, that if any person or persons shall and doth rake, pick or any other way gather any cranberries on any of the lands or meadows belonging to the proprietors of Montauk or the town commons at any time before the second Tuesday in October next, ensuing at sunrise, he, she, or they so offending shall forfeit and pay the sum of eight shillings, current money of New-York, per bushel, to be recovered before any Justice of the Peace in and for the county of Suffolk."

There are, of course, many commercial cranberry bogs on Long Island, notably in the region between Manorville and Riverhead that are larger than any at Montauk. But as wild growths, the Montauk bogs are the most extensive.

In this region there is a curious relic of introduction in a large grove of *Ailanthus* trees at the southeastern edge of Reed pond. It comprises at least three acres and the trees are vigorous. Borings from their trunks indicate approximately even age which appears to average about sixty-five years.

FIGURE 20. Wind wrenched specimen of the sour gum (*Nyssa sylvatica*) with an Osprey's nest. (Photograph by Barrington Moore) See also figure 17.

FACTORS OF CONTROL.

THE CLIMATE.

The most active determinant in the recent development of the Montauk vegetation appears to be the wind, of which there is a greater movement there than at any other point on the Atlantic coast.* Indeed the wind is so terrific, of such long-continued gale force, that after a few visits one is apt to think that the wind is the only factor controlling the present distribution of the vegetation.

While there is no weather station at Montauk, the figures for Block Island, which is sufficiently close [16 miles] to warrant the statement that the conditions are about the same, have been studied. An average over a period of years shows that the total wind movement at Montauk (Block Island) is 155,975 miles per year. This is nearly double that of the middle of the Island, the nearest Weather Bureau station for which is New Haven, and which shows an annual wind movement averaging slightly over eighty thousand miles. In other words, the wind blows twice as much at Montauk

* It should be said that Sandy Hook is a close second to Montauk, perhaps because of the funnel-like action of the Hudson Valley, in conjunction with the normal sea breezes.

as it does at Port Jefferson, for instance. During many months the wind movement at Montauk averages thirteen thousand miles (about six thousand at Port Jefferson) and hourly velocities of 60, 65, 72, 74 and 80 miles are not uncommon, while the wind has been known to blow as much as 84 and 86 miles an hour during severe storms. The high record at Port Jefferson is 61 miles an hour.

Another feature of the wind at Montauk, surpassing all other stations along the Atlantic coast, is that there average 109 separate winds in each year, of over fifty miles an hour velocity. Even comparative periods of calm, punctuated by such gales, must have a profound effect upon the vegetation.

These separate winds that blow over fifty miles an hour come more frequently, of course, during the winter months. Eighty of them come during December, January, February and March, while the others are scattered through the rest of the year, June and July excepted, which appear to be, on the average, free from them. The scarcity of evergreens,—there is only a single stunted pitch pine, and very few cedars,—may well be due to the bunching of these winds during a period when, unlike deciduous trees, their transpiration demands are most difficult to meet.

Most of these figures of wind movement are taken from an article by Spencer Lee Trotter on "Local peculiarities of wind velocity and movement along the Atlantic seaboard,—Eastport, Me., to Jacksonville, Fla." which appeared in the *Monthly Weather Review* for November 1920, and from earlier records of the Weather Bureau. These records are too copious to quote here, but summarizing from them shows the following for the wind movement at Block Island (Montauk):

YEARLY WIND MOVEMENT AT MONTAUK

1912	159,591 miles	1918	153,774 miles
1913	153,982 "	1919	155,084 "
1914	159,979 "	1920	160,848 "
1915	154,313 "	1921	155,801 "
1916	160,504 "	1922	155,488 "
1917	156,203 "		

It should be remembered in this connection that all the figures from Montauk (Block Island) are based on instruments only forty-six feet above sea level, which is lower than at any of the coastal stations which Mr. Trotter has tabulated. Many of the hills at Montauk are at least twice that height above sea level, and a few three times that height. If the measurements of Stevenson as to the increase of wind with altitude operate

at Montauk as they did at Edinburgh,* then there may well be an increase of from 20% to 50% in wind movement over the greater part of the Downs, and practically all the vegetation has been subjected to wind movement considerably in excess of the figures given in the table.

FIGURE 21. Wind wrenched specimen of white oak (*Quercus alba*) on windward edge of Hither Woods. There are hundreds of such specimens along the seaward edge of the woods, which extends about four miles west-southwest of Fort Pond.

But not only is the strength and distribution of the winds that sweep over Montauk of significance,—their direction is even more so. Summarizing again from the Weather Bureau records, it transpires that except for the occasional 'Northeaster,' the bane of boatman, all these great winds

* Journ. Scot. Meteorl. Soc., new series 5: 348. 1880; quoted by Schimper, not seen by me.

are west, northwest or southwest. For days on end the white-capped Fort Pond Bay, just off the village, and the thundering of the surf on the seashore are ever present reminders of the force and steadiness of these westerly and southwesterly breezes. In the winter they are apt to be northwesterly.

Quite as much as these marine reminders of the wind is the peculiarly effective response of the vegetation to it. Gnarled and often dead trees (Fig. 21), or trees and shrubs that are normally many feet tall but at Montauk are prostrate or stand up only a few inches, are mute evidence of this ceaseless power of the wind. Other rather striking reminders of this are the individual response of certain herbs, such as prostrate habit, cushion-like clumps, or one-sided growth, and the failure of certain shrubs and all trees to grow on the tops of the Downs, and their practical confinement to the bottoms of kettleholes or other protected places among some of the taller Downs.

Some quantitative expression of the effect of this wind on the vegetation is so far unavailable, except the records of the rate of growth of the scarlet oak on the windward and leeward sides of the Hither Woods, an account of which will be found in the section, "Hither Woods" (Figs. 18 and 19).

But beyond the purely mechanical effect, which is everywhere obvious at Montauk, practically nothing is known of the effect on transpiration and other processes of plant activity of violent gales.*

Once, in 1625, a great storm visited all the northeastern Atlantic coast and reports, mostly apocryphal, tell of severe damage. But on September 23, 1815, a southeast gale of such intensity as to destroy "one half of the forest trees and fruit trees," occurred and there are ample records of it.† The Long Island *Star*, a weekly newspaper, quotes in its issue of October 4, 1815, a letter from a correspondent at Sag Harbor, dated September 24:

* There are many references to the mechanical effects of wind on vegetation, particularly of violent storms or hurricanes, notably: by C. T. Simpson, Plant World **6**: 284–285. 1903; by G. H. Kroll, Bot. Centrl. Beih. **30**[1]: 122–140. 1913; by B. F. Hoyt, Amer. Nat **20**: 1051–1052. 1886; by G. Eisen, Zoe **3**: 1–11. 1892; by H. von Schrenk, Trans. St. Louis. Acad. Sci. **8**: 25–41. 1898; by J. Dufrenoy, Comp. Rend. **69**: 174–175. 1917. There is also an account of the effect of the wind on the trees along the Californian coast in W. L. Jepson's "Silva of California," **2**: 40–44. 1910. Some of these and many others are summarized in Schimper's monumental "Plant Geography" (English version, Oxford, 1903.) More recently, Leonard Hill (Proc. Royal Soc. Ser. B **92**: 28–31. 1921) has written on "The Growth of Seedlings in Wind."

† I am indebted to Mr. Jonathan Gardiner, now in his eightieth year, for first calling my attention to this. Mr. Gardiner, who lives at Easthampton, lived for many years on Gardiner's Island, and has heard several first hand accounts of this storm from people who lived at the time. For the possible effects of salt laden winds destroying vegetation during this storm see also an article by J. B. Beck, Am. Journ. Sci. **1**: 388–397. 1819.

"Yesterday we experienced one of the most tremendous gales ever experienced in this climate. It blew a hurricane. Trees are strewed in every direction about our streets. . . . The lighthouse on Montauk is so injured that no light can be kept in it until the lantern be repaired." The same paper said, on October 11, and on October 18, that the lighthouses on Gull and Little Gull Islands were also out of commission, due to the storm.

Mr. Gardiner reported to the writer that men who had visited Montauk after the storm told him that much timber had been destroyed at the Point Woods, and in fact, all over Montauk Point. But the blowing down of trees such as unquestionably occurred can not have made very much difference in the relative *proportion* of grassland and forest at Montauk. The records already quoted show that from the earliest days there had always been, within historic times at least, large areas of Montauk in grassland. If anything, this storm would tend to increase the area of this. It may well have blown down the tallest trees at the Point Woods, none of which at present is over forty or fifty feet in height,—most of them much lower.

While the wind is the most striking of the climatic features of Montauk, the peninsula is both cooler and drier than any other part of Long Island, In an account of the climate of Long Island as it is related to the vegetation. which will be presented elsewhere, the details of these factors are given. Summarizing from them the Montauk records show the following:

TEMPERATURE

Mean temperature	49.5°	which is 95.1% of the warmest Long Island station.
Yearly effective temperature, = total above 43°	3536°	which is 80.7% of the warmest Long Island station.
Effective temperature before May 31	319°	which is only 49.1% of the warmest Long Island station, and is the explanation of the "late spring" at Montauk, which, in the flowering of certain plants is from ten to fifteen days behind Brooklyn.
Frostless period	218 days	which is longer than for any other Long Island station.

The retarding of spring and the length of the growing season at Montauk are both affected by the temperature of the sea water. This is from 6 to 10° cooler at Montauk than at the western end of Long Island during the period April 15 to June 9, while during the period from November 15 to December 25, it is usually slightly warmer than for the western end of the

Island.* Full details of the temperature of the sea water at the eastern and western ends of Long Island will be published later in another connection.

The Livingston and Shreve direct summation of normal daily mean temperature for the period of the frostless season shows for Montauk (Block Island):

Above 0° F.	Above 32° F.	Above 39° F.†	Above 50° F
12,946	5,970	4,444	2,264

RAINFALL (INCLUDING SNOW)

Annual	41.79 inches,	which is 89% of the wettest Long Island locality.
Amount of rainfall during the period of effective temperature	27.02 inches,	which is 91% of the wettest Long Island locality during this period.

EVAPORATING POWER OF THE AIR.

Of the different types of evaporimeter it was decided to use the Livingston black and white atmometer, largely because the readings from them are more easily comparable to the results of other workers.

All the records were taken with instruments mounted in the usual way, but the bottles in every case (except one to be noted specially) were buried up to the neck. Some of the records were taken before the mercury valve to prevent intake of water had been proposed, but in these records daily readings were made for rather brief periods in September 1919, and May 1920. During 1921 the instruments ran continuously from July 15 to September 24, and in 1922 from July 27 to August 18. Both the 1921 and 1922 readings were made at intervals of several days, with mercury valve instruments.‡ In all cases the accompanying graphs (Figs. 22–25) have been translated to the rate per day (the number of cc. per day) of evaporation.

* There is a brief account of the sea breeze on eastern Long Island and of the effect of this cool sea water on the climate of the Island, both by Ernest S. Clowes of Bridgehampton in *Monthly Weather Review* for July 1917. They show very clearly the effect on the temperature, particularly near the shore, of the sea breeze blowing in from the cool water.

† The nearest figure to the so-called "effective temperature" used above, which is merely the addition of all the degrees of temperature in excess of 43°, which has been used by many other workers as a basis.

‡ The 1921 instruments were supplied with a mercury valve held in place by glass wool. A decided improvement in this was devised by Mr. Frederick A. Musch of New Haven, who kindly made a series of readings for me in the pitch pine region at North Haven, Connecticut. Mr. Musch's ingenious modification of the usual tubing made the mercury valve a most satisfactory device for the Livingston atmometer. See *Science* 57: 26–28. 1923.

During 1919 and 1920 the instruments were set out as follows:

1. On open exposed Downs.
2. At the contact of the Downs with a wooded kettlehole, and about six feet from the wooded fringe of it.

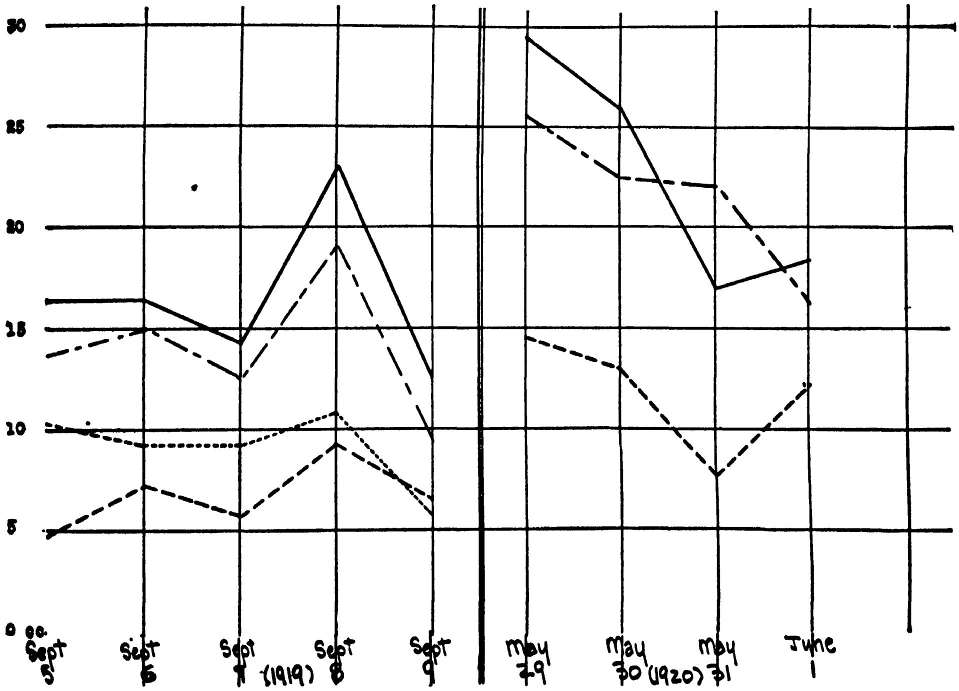


FIGURE 22. Evaporation, White Atmometers. Montauk, Long Island. September 5–9, 1919. May 29–June 1, 1920.

On open downs. ————————

At their contact with wooded kettleholes. — — — — — — — —

In Bayberry thicket. - - - - - - - - - - - - -

Under canopy of wooded kettlehole. - — - — - — - — - —

Fire had destroyed the bayberry thicket between the 1919 and 1920 readings, so this station is omitted from 1920 graph.

3. In the middle of a bayberry thicket, but as none of the bushes was over one foot high, the instruments were set so that they were not shaded by them.
4. On the forest floor of a wooded kettlehole.

As these 1919 and 1920 graphs show (Fig. 22) there is, as might be expected, a steady increase in the rate of evaporation from the wooded kettlehole to the open Downs, but what they do not tell us is that nowhere on Long Island, as subsequent readings have proved, is there such a violent

contrast between the site producing a forest and a closely adjoining one unable, or only very tardily able to do so. Most other Long Island atmometer readings show, of course, a decided difference in the evaporating power of the air as between [usually artificial] openings and the forest. But at Montauk, as these and the graphs of 1921 show (Fig. 24) that difference is often two to three hundred per cent. There is involved in the kettlehole readings, as in all forest atmometer records, the question of how much they reflect the effect of the forest canopy, and how much the actual difference in site. In other words, whether the forest readings indicate a contributing cause or merely the effect of the forest itself. An interesting sidelight on this is furnished by the 1920 figures, where, because of the lateness of spring at Montauk, the forest canopy had only just begun to really intercept the sunlight. Yet the difference between the Open Downs station and the wooded kettlehole, even during this period, is substantially what it proved to be when the canopy had reached its midsummer density.

The graph for 1921 (Fig. 24) shows an even greater difference between the open Downs and the wooded kettlehole, in some weeks the difference being over five hundred per cent. Taking the figures of the wooded kettlehole as indicative of a reasonably favorable environment for forest growth and reproduction, those of the open Downs suggest an environment at least five times as severe, so far as evaporation is concerned. Such a contrast of environmental conditions, even excluding the occasional fires that sweep over the Downs, would be more than sufficient to explain the mutual exclusiveness of these two dominant sorts of plant covering at Montauk. The shade of the wooded kettlehole prevents the entrance of grassland (of course certain species of *individual* grasses are in all kettleholes, and a few Downs species occasionally do get into them), while the exposure of the Downs to such conditions as these graphs show, effectually prevents nearly all encroachment from the wooded kettlehole out to the open.

One or two features of the atmometer readings of 1921 demand special mention. While atmometers are not supposed to be a measure of wind velocity that is included in the totality of climatic factors which beats upon these instruments. In the case of Montauk the wind velocity is greater than for any other Lond Island station, where atmometer readings have been made. The total evaporation from white atmometers at these different places on the Island, all in the open, and exposed simultaneously was, from July 15 to September 24, 1921:

Montauk	1459.9 cc. =	100%
Crystal Brook, North shore opposite New Haven	1352.2 cc. =	92.6%

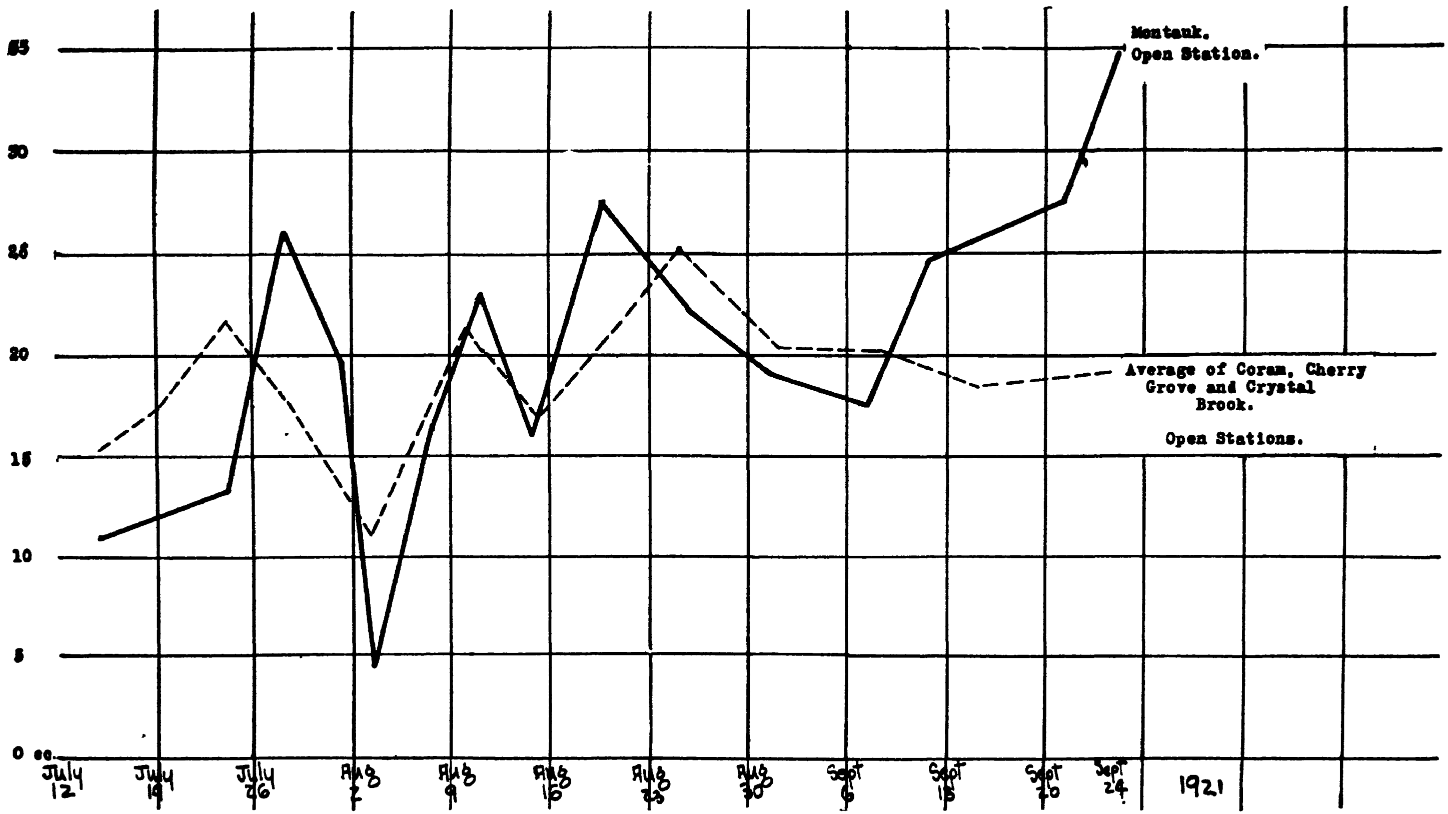


FIGURE 23. White atmometer readings on the Montauk Downs, compared to the open readings from the central portions of Long Island, which have been averaged. 1921. Readings are in cc. of evaporation per day. The atmometer stations in central Long Island which were averaged were at Coram, Cherry Grove and Crystal Brook. See text for details.

Cherry Grove, on Fire Island Beach	1311.4 cc. =	89.8%
Coram, in center of Long Island	1234.2 cc. =	84.5%

Crystal Brook is in the center of a heavy oak forest and the open station there was selected because it was sheltered from the drying southwest wind of summer. Coram is in the pitch pine region and exposed to this wind, while Cherry Grove is out on the barrier beach, and in full exposure to the winds from the sea. And yet the figures are all within 16% of one another, so that while the conditions of Montauk, judging by the vegetation, are totally different from the other localities, this lack of forest growth, in so far as it is due to wind, is certainly not expressed by the readings of the white atmometers. While the evaporation is higher than for anywhere else on Long Island, it is not so much higher as the vastly different vegetative condition of the Point would suggest it should be.

The accompanying graph (Fig. 23) shows by unbroken and broken lines the details of how the white atmometers in the open at Montauk differed from the other Long Island stations in the open, which have been taken at Coram, Crystal Brook and Cherry Grove and averaged.

Black atmometers were exposed in all the stations, two feet from the white instruments, and appear from the readings to be a more sensitive and perhaps better indicator than the white ones. While neither the white nor black atmometers profess to be an accurate measure of transpiration, the curve of either or of their difference (so called solar radiation) has a very general correspondence to the transpiration of twelve trees as shown by Bates.* To that extent at least the Livingston atmometers, while not a measure of transpiration are a pretty good indicator of its variation over longer or shorter periods, and in average conditions of growth where wind velocity is more normal. In fact, Burns has shown† that "Evaporation-transpiration coefficients based on unit of dry weight . . . show that response of the plants agree more closely with the black atmometer than with the white atmometer." The curves in the paper by Bates, already referred to, also show greater correspondence between the Livingston black atmometer and transpiration, than with any other type of evaporimeter with which he experimented, except the all-metal device which he describes there.

In the light of the statements of Burns and Bates the evaporation from the black instruments at Montauk during the four day period July 25–28

* Bates, C. G. A new evaporimeter for use in forest studies. Monthly Weather Review **47**: 283–294. 1919.

† Burns, G. P. & Hooker, F. P. Studies in tolerance of New England trees II. Relation of shade to evaporation and transpiration in nursery beds. Bull. Vermont Agr. Exp. Sta. **181**: 235–262. 1914.

inclusive (1921) is instructive. As the graph shows, the rate per day of the white instrument for that period was 26.5 cc. During the same time the black instrument touched 49.3 cc., and in fact throughout the season, the black, as would be expected, was consistently higher than the white. But weather conditions during those four days ought not to have produced such black readings, if current theories about that instrument are correct. At Montauk this was the condition as to the main climatic features of these four days, during which no rain fell.

1921	Max. Temp.	Total wind Movement and Direction	Vapor Pressure Inches	Actual sunshine hours	Total Possible sunshine hours
July 25	74	442 mi. SW	.646	5.1	14.6
26	79	389 mi. SW	.732	10.9	14.5
27	77	472 mi. SW	.700	6.0	14.5
28	76	627 mi. SW	.715	11.3	14.5

During two days of that period sunshine did not exceed 76% of the possible, while during the other two it was not over 40% of the possible and yet it is precisely sunshine that is supposed to affect the black instrument most acutely. As the graph shows, this four day period had a higher rate of evaporation than any other part of the season in spite of a partial lack of sunshine during two of the days, and a serious lack of it on the other two. But during those days the total daily movement of wind, and the hourly velocity, were higher than for many days after. For the sake of the record, I append the rate of the black atmometer on the Montauk Downs, the maximum temperature, the vapor pressure, and wind velocity per hour, for the "high spots" on the 1921 graph, together with actual and possible amount of sunshine.

Reading ending	Mean maximum temp. of each period.	Evaporation per day in cc.	Direction and highest velocity of wind during period of atmometer reading	Average vapor pressure inches	Actual sunshine hours*	Possible sunshine hours
July 28	76	49.3	SW 40 mi. an	.698	8.3	14.5
Aug. 12	75	35.8	SW 32 hour	.617	8.7	13.9
Aug. 18	73	40.0	SW 34	.552	7.5	13.7
Sept. 9	76	43.0	SW 22	.556	9.1	12.8
Sept. 24	71	45.0	SW 42	.497	11.2	12.1

* The actual hours have been calculated on the basis of taking the readings for each day of the period ending on the dates in the left hand column, and averaging them. The figure, then, means that during the period of atmometer readings ending with each date, each *day* had on the average the number of hours sunshine given in the next to the last column.

Taking into consideration that the days were considerably shorter toward the end of the readings, it is certainly of significance that at each period of high winds the black instrument shows marked increase in its rate of evaporation. And if, as Bates and Burns have shown, it is a better measure of actual transpiration than the white instrument, it may well be that from the peak readings of the black instruments at Montauk we get the best expression of the most unfavorable environmental conditions on the Downs, and the best picture of, at least the probable effect of wind as it keeps down the establishment on these Downs of almost everything but grassland and bayberry thickets. No one who has visited Montauk when one of these southwest summer winds is blowing, and the temperature is high (for Montauk) can ever fail to be impressed with the unfavorable effect it must be having on transpiration and growth. Coupled with soil conditions, to be described presently, it is undoubtedly the chief factor in keeping things as they are on the Downs.

This high rate of evaporation and probably also of transpiration coinciding with high winds does not conform to the results of Briggs and Shantz.* They found that evaporation and transpiration were much more sensitive to sunshine than to wind, and in fact discount the latter as a factor of importance. That conclusion appears to fly in the face of most practical gardeners' notions of the effect of wind on transplanted seedlings, where, even if the ground be kept moist, wilting is more apt to occur in a high wind than during a period of calm. An examination of the papers cited shows that the highest wind velocity reached in their experiments is 13.5 miles per hour (given by them as 6 meters per second). It may well be that such low velocities are much over-ridden by other factors such as sunshine, as all their graphs show a remarkably close correlation between transpiration, evaporation and sunshine, and almost no correlation between these and changes of wind velocity.

The wind, however, scarcely begins to blow at Montauk until it reaches at least twenty-five miles an hour, and it certainly appears from the records that at velocities of more than that it does have a decided effect. Nor can the "high spots" in the black readings be attributed to specially clear days with a maximum of sunshine. The accompanying tabulations of the conditions and the graphs show that high evaporation from the black instru-

* Jour. Agr. Res. 5: 583–649. 1916, on "Hourly Transpiration Rate on Clear Days as Determined by Cyclic Environmental Factors;" *loc. cit.* 7: 155–212. 1916, on "Daily Transpiration during the normal growth period and its correlation with the weather;" or with *loc. cit.* 9: 277–292. 1917, on "Comparison of the hourly evaporation rate of atmometers and free water surfaces with the transpiration rate of *Medicago sativa.*"

ment* may or may not coincide with the greatest possible sunshine, while it nearly always does with high wind.

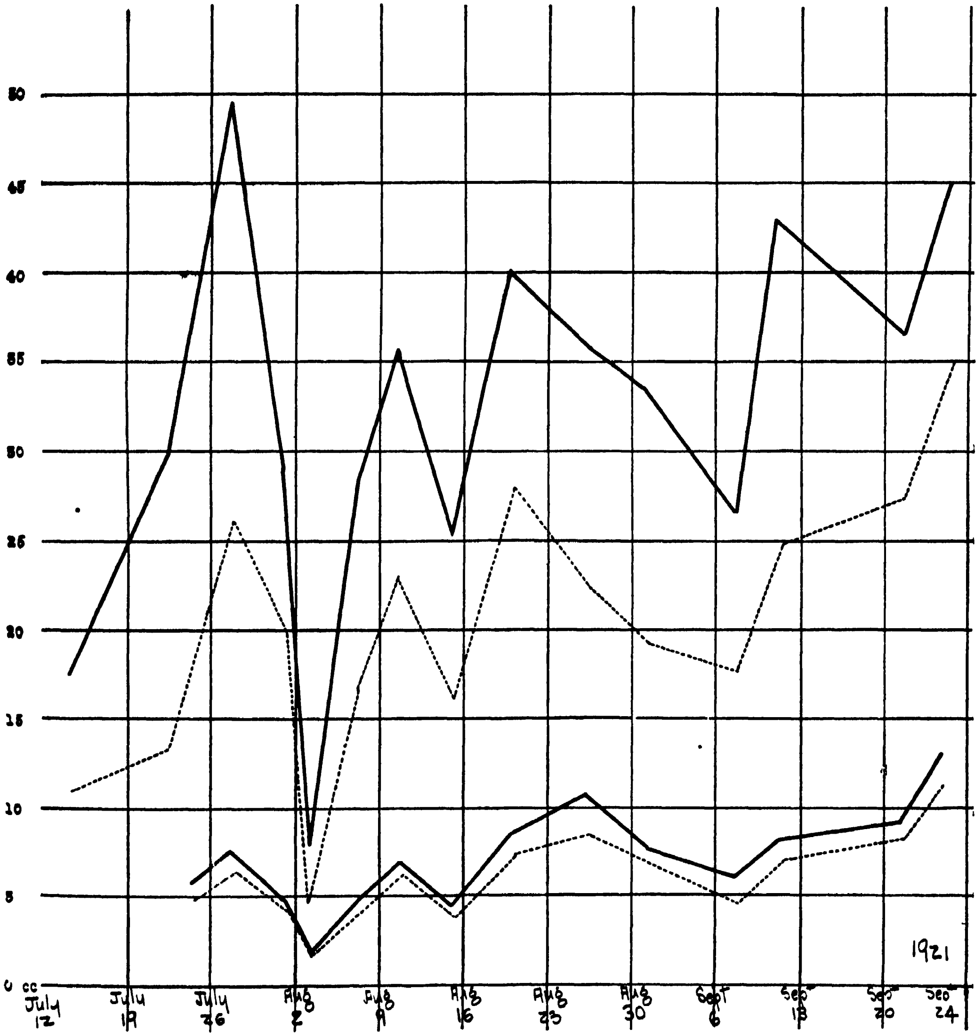


FIGURE 24. Montauk atmometer readings, 1921. Upper series are on the open Downs, lower in the shade of wooded kettlehole. Black lines = black instruments, dotted lines = white instruments. The records are reduced to the cc. of evaporation per day.

* And also from the white instruments. But the blacks show much greater *excess* of evaporation over the whites during high winds than at other times. The basis of the argument in a nut shell is that black instruments reflect transpiration rates better than white ones, and if this is true, as Bates and Burns would have us believe, then high wind movement, as reflected by the meteoric rise of the black instrument, does so affect transpiration as to be one of the chief limiting factors.

An examination of the graph of evaporation (Fig. 24) and of the details of sunshine together with wind velocity, shows, during the period August 19–25, 1921, a good example of the fall of the evaporation rate of the black instrument, in the face of better than the average rate of insolation. The possible amount of sunshine during this period is 13.5 hours per day. The actual sunshine for the period averaged 12.4 hours, which more nearly approaches the possible amount than for any of the peak periods of the black instrument. In the face of these seven days, when sunshine was nearly at its maximum, there is, as the graph shows, a steadily falling rate of evaporation from the black instrument. No rain fell during the period, and the wind averaged but 22 miles per hour, while the mean maximum temperature for the seven days was 70°. Comparison of these conditions with those of the September 24 atmometer readings confirms the point. The maximum temperatures then were one degree cooler, sunlight about one hour less, and yet presumably, under the stimulus of a wind of 42 miles an hour from the southwest, the black instrument climbed to 45.0 cc. of evaporation per day.

The maximum temperature, rainfall, vapor pressure, wind velocity and prevailing wind direction together with the possible and actual amount of sunshine, for the period of these 1921 readings is here recorded, most of the details of which have been kindly placed at my disposal by the Weather Bureau station at Block Island.

Evaporation Black and White Atmometers and Daily Maximum Temperatures, Precipitation, Vapor Pressure, Direction and Velocity of Wind, Hours Possible Sunshine and Hours Actual Sunshine.
Montauk Downs 1921

Date	Max. Temperature	Rainfall	Wind velocity	Wind direction	Hours Possible Sunshine	Hours Actual Sunshine	Vapor Pressure Inches	Evaporation per day in cc.	
								Black	White
July									
15	74	.52	38	S W	14.8	0.9	.670		
16	75	.01	22	N E	14.8	6.7	.569		
17	75		19	S	14.8	12.1	.631		
18	74		26	SW	14.8	9.2	.646		
19	75	.24	22	S	14.7	1.2	.700	29.8	13.3
20	79	1.28	25	W	14.7	10.7	.639		
21	68		32	N E	14.7	2.2	.568		
22	71		16	E	14.7	8.9	.530		
23	73		16	E	14.6	11.7	.575		
24	76		24	S W	14.6	14.6	.676		

Date	Max. Temperature	Rainfall	Wind velocity	Wind direction	Hours Possible Sunshine	Hours Actual Sunshine	Vapor Pressure Inches	Evaporation per day in cc.	
								Black	White
July									
25	74		25	S W	14.6	5.1	.646		
26	79		24	S W	14.5	10.9	.732	49.3	25.9
27	77		25	S W	14.5	6.0	.700		
28	76		40	S W	14.5	11.3	.715		
29	79	.39	24	S W	14.4	0.7	.699		
30	75		14	S E	14.4	10.8	.676		
31	76	1.06	52	S	14.4	0.0	.702	28.7	19.5
Aug.									
1	68		32	W	14.3	4.0	.461		
2	65	.37	23	S W-W	14.3	0.0	.543	7.8	4.7
3	66	.11	18	F	14.3	0.0	.520		
4	75		13	S E	14.2	10.9	.553		
5	75		17	S W	14.2	14.2	.605	28.4	16.5
6	73		22	S	14.2	14.2	.602		
7	76		24	S	14.1	5.4	.716		
8	75	.29	24	W	14.1	6.9	.627		
9	74		18	W	14.1	14.1	.477	35.8	22.9
10	76		16	S W	14.0	14.0	.638		
11	76		24	S W	14.0	6.8	.692		
12	75	.08	32	S W	13.9	1.7	.661		
13	70		23	S E	13.9	3.3	.610	25.3	16.0
14	75	.22	33	S W	13.8	0.0	.709		
15	72		34	N W	13.8	13.8	.417		
16	74		28	W	13.8	13.0	.494		
17	74	.02	29	S W	13.7	1.7	.596		
18	75	1.96	35	S W	13.7	1.8	.701	40.1	27.6
19	76		21	W	13.6	13.6	.532		
20	75		29	S W	13.6	9.3	.661		
21	70		34	E	13.6	13.6	.461		
22	71		22	NW-NE	13.5	10.0	.455		
23	70		12	E	13.5	13.5	.402	35.6	22.2
24	69		14	E	13.4	13.4	.471		
25	71		28	N E	13.4	13.4	.517		
26	70		32	N E	13.4	13.4	.450		
27	67		20	NE-E	13.3	12.4	.454		
28	69		12	E	13.3	3.1	.513		
29	72		26	S W	13.2	4.8	.625		
30	76		32	S W	13.2	7.6	.676	33.6	19.1
31	75		24	E	13.2	5.8	.631		
Sept.									
1	73		16	E	13.1	13.1	.589		

Date.	Max. Temp-era-ture	Rain-fall	Wind veloc-ity	Wind dir-ection	Hours Possible Sunshine	Hours Actual Sunshine	Vapor Pressure Inches	Evaporation per day in cc.	
								Black	White
Sept.									
2	77		25	S W	13.0	4.4	.716		
3	83		30	W	13.0	11.8	.654		
4	72		28	N E	13.0	9.9	.530		
5	69		24	E	13.0	11.7	.512	26.4	17.5
6	73	.01	16	S E	12.9	3.7	.676		
7	73	.03	18	E	12.8	7.4	.616		
8	74		12	N	12.8	10.5	.557		
9	76		12	N E	12.8	9.4	.496		
10	74		22	S W	12.7	12.7	.595	43.0	24.6
11	75		21	S W	12.7	9.8	.631		
12	74	.01	11	S	12.6	0.0	.676		
13	76		27	W	12.6	9.8	.531		
14	66		26	N	12.5	6.3	.408		
15	72	.06	26	S W	12.5	10.6	.538		
16	67		19	N E	12.4	10.2	.439		
17	71	.09	30	S-S W	12.4	3.2	.560	36.3	27.4
18	75	.01	36	W	12.4	8.4	.525		
19	66		36	N W	12.3	12.3	.376		
20	65		20	N E	12.2	8.7	.385		
21	68	.19	32	S E	12.2	0.0	.465		
22	74	.15	42	S W	12.2	9.4	.569		
23	74		30	S W	12.1	12.1	.505	44.9	34.8
24	69		13	N	12.1	12.1	.419		

The 1922 readings, which were only made on the open Downs, extend from July 27 to August 18. As the accompanying graph (Fig. 25) shows this happened to be a much less critical period than the previous season, and consequently does not have the significance of the much higher readings of 1921. As a record of the general climatic condition during 1922 I append a detailed weather report by Lieut. Roger W. Autry, the Camp Signal Officer at Camp Welsh. The artillery regiments quartered at Montauk during the summer of 1922 kept a meteorological tent in operation, with observations taken at 8:30 A.M. and 2:00 P.M. It is from these records which are complete except for Saturday afternoons and Sundays, that the following is taken.

EVAPORATION BLACK AND WHITE ATMOMETERS AND DIRECTION AND VELOCITY OF THE WIND, TEMPERATURE, VAPOR PRESSURE, AND SKY.
MONTAUK DOWNS, JULY 21–AUG. 18, 1922.

Date	Direction and Velocity of the Wind	Mean Temperature	Vapor Pressure (inches)	Sky	Evaporation per day in c.c	
					Black	White
July						
20–AM	E–2	71.0	.732	fog		
20–PM	E–10	70.0	.707	cloudy		
21–AM	NW–8	67.0	.638	partly cloudy		
21–PM	S–6	79.8	.684	partly cloudy		
22–AM	SW–8	71.0	.732	clear		
22–PM	——	——	——	——		
23–AM	——	——	——	——	24.1	20.6
23–PM	——	——	——	——		
24–AM	N–8	72.0	.757	clear		
24–PM	NE–6	74.0	.732	cloudy		
25–AM	NE–13	64.2	.575	cloudy		
25–PM	SE–17	68.0	.684	cloudy		
26–AM	SW–8	66.5	.638	partly cloudy		
26–PM	SE–12	69.7	.661	clear		
27–AM	NW–13	66.3	.616	cloudy		
27–PM	SSE–15	73.2	.732	cloudy		
28–AM	SSE–6	68.2	.684	cloudy		
28–PM	SSE–7	70.8	.732	cloudy		
29–AM	NW–14	67.0	.616	partly cloudy		
29–PM	——	——	——	——		
30–AM	——	——	——	——		
30–PM	——	——	——	——		
31–AM	SW–8	69.0	.661	clear		
31–PM	SSE–10	76.1	.757	clear		
August					29.4	18.6
1-AM	N–8	67.0	.707	fog		
1–PM	——	——	——	cloudy		
2–AM	N–5	67.0	.661	rain		
2–PM	NE–7	64.8	.616	cloudy		
3–AM	N–7	65.6	.595	cloudy		
3–PM	SE–5	68.1	.638	cloudy		
4–AM	ENE–7	66.8	.638	cloudy		
4–PM	ESE–8	71.8	.707	partly cloudy		
5–AM	NW–7	69.5	.684	clear		
5–PM	——	——	——	clear		
6–AM	——	——	——	cloudy	24.0	15.7
6–PM	——	——	——	clear		
7–AM	SSW–12	71.5	.745	cloudy		
7–PM	SSW–16	74.9	.757	cloudy		

Date	Direction and Velocity of the Wind	Meaa Tempern-ture	Vapor Pressure (inches)	Sky	Evaporation per day in c.c.	
					Black	White
July						
8-AM	SW-14	69.1	.661	rain		
8-PM	SW-9	71.6	.757	cloudy		
9-AM	NE-18	62.	.517	cloudy		
9-PM	NE-15	66.3	.536	cloudy	24.0	15.7
10-AM	NE-16	63.7	.499	cloudy		
10-PM	NE-14	67.6	.536	cloudy		
11-AM	NE-20	63.1	.432	cloudy		
11-PM	NNE-22	63.0	.482	cloudy		
12-AM	NE-16	63.1	.575	rain		
12-PM	——	——	——	rain		
13-AM	——	——	——	partly cloudy		
13-PM	——	——	——	partly cloudy		
14-AM	W-9	69.8	.684	clear		
14-PM	SW-13	76.0	.707	clear		
15-AM	SSW-5	68.8	.684	fog	27.2	17.7
15-PM	SW-12	71.8	.732	fog		
16-AM	SW-9	70.8	.707	clear		
16-PM	SW-21	74.0	.757	clear		
17-AM	NW-4	75.0	.783	clear		
17-PM	S-4	80.5	.783	partly cloudy		
18-AM	SW-14	70.0	.732	clear		

Lack of wind velocity, such as the table shows, is unprecedented for Montauk, and, if the black instruments are as sensitive to wind as the 1921 readings appear to indicate, their low rate of evaporation during the 1922 period is understandable. So far do the readings of the black or white instruments depart from the normal that the total evaporation from the white atmometer in the open is actually exceeded by a similarly exposed instrument at Coram. There the record from July 27 to August 28 totalled 179.4 cc. more than at Montauk! This excess at Coram is undoubtedly due partly to higher temperature, as the central pine-barren region, at least so far as maximum temperatures are concerned, is always considerably warmer than Montauk. It is partly due also to the lower humidity at Coram. Montauk, surrounded by water, is, in the absence of its usual gales, a decidedly humid region, and during the 1922 readings, as the detailed record shows, the wind never reached a velocity of even twenty-five miles an hour. A glance at the velocities during the 1921 high readings will confirm the statement there hazarded that wind velocity and the rate

of evaporation from the black instrument, if not transpiration itself, are rather closely correlated.

I am glad to make acknowledgments to Dr. Robert L. Dickinson and to Miss Maria B. Fairbanks for making many of the readings of the atmo-

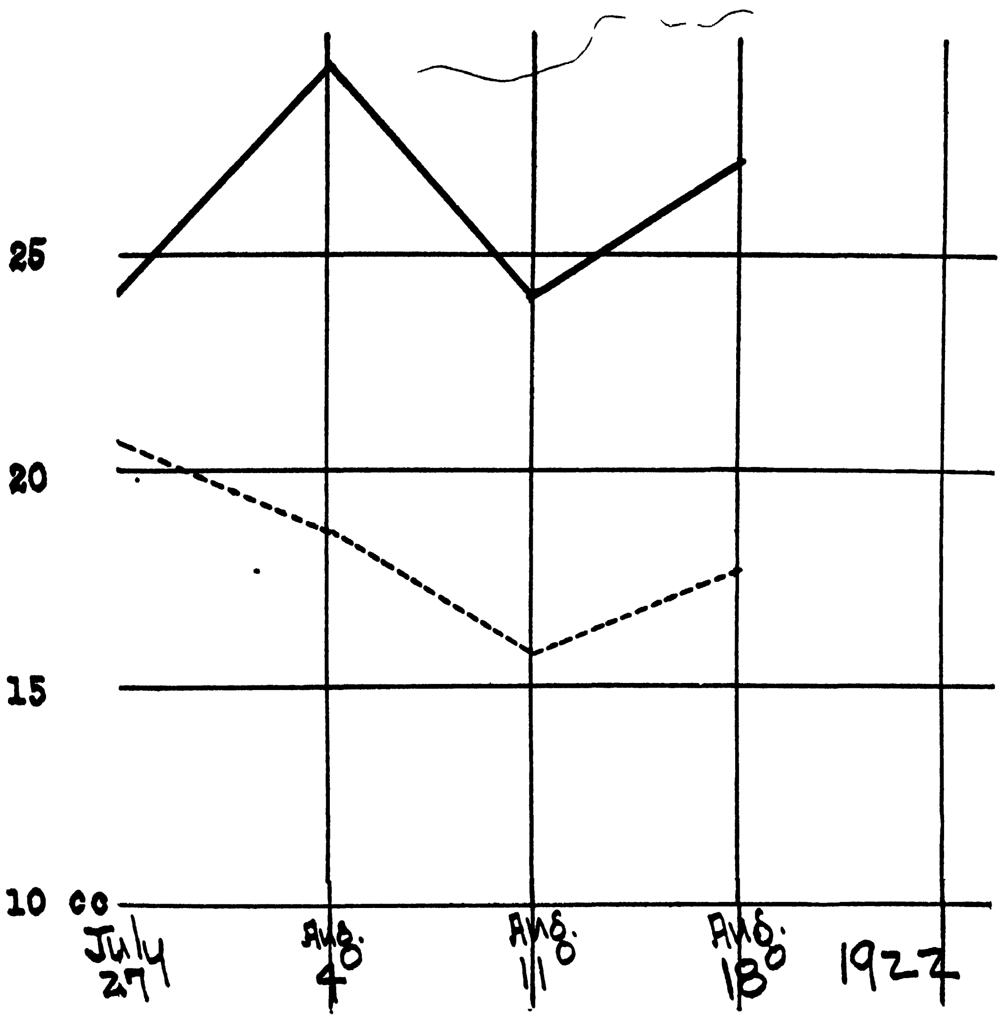


FIGURE 25. Atmometer records on Montauk Downs in 1922. Black line = black instrument, dotted line = white instrument. The records are reduced to the number of cc. of evaporation per day.

meters; to Lieut. R. W. Autry for supplying the meteorological data during the 1922 readings; and to Mr. George W. Eddey, in charge of the U. S. Weather Bureau at Block Island, for many courtesies. All this voluntary assistance has been most helpful in accumulating the data on the climate of Montauk.

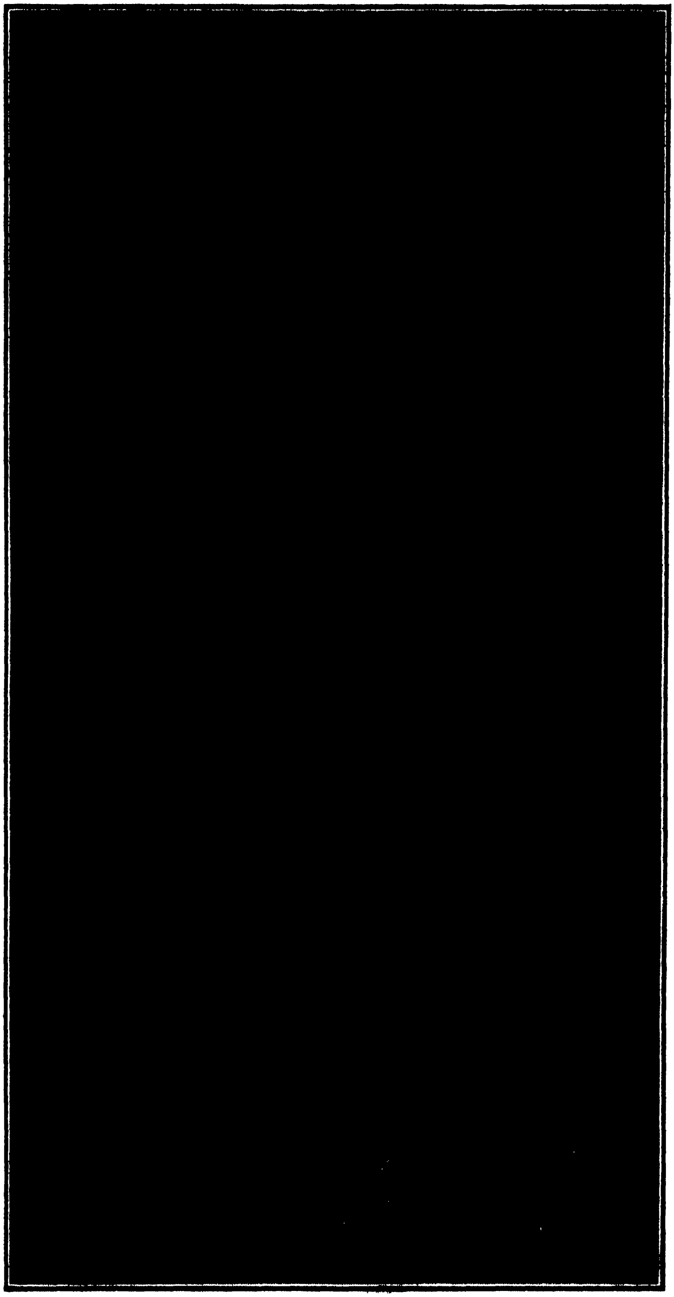


FIGURE 26. Roots of *Myrica carolinensis*, near Ditch Plain Coast Guard Station. The roots penetrated 36 inches of fine sand. (Photograph by Barrington Moore.)

Soils.

It is needless to go into the geology of Montauk* more than to say that all of the surface of the peninsula is made up of glacial till of the Ronkonkoma Moraine, and from this, of course, all the soils of Montauk have been derived.

This geologically similar material is by no means matched by a similarity of soils. Considering first the mineral soil, which is soil that remains unmodified by the vegetation,—the subsoil of the gardeners,—it is at once obvious that this differs in different parts of Montauk and under different vegetative types.

Disregarding boulders, small stones and coarse gravel, the available subsoil appears to be, under the typical Downs, a mixture of about 85% coarse yellow sand, and 15% of fine sand with sometimes a slight admixture of silt. It is into such a substratum that the deeper rooted perennials, such as *Baptisia tinctoria*, and all the shrubs, always penetrate (Fig. 26). And of all the Montauk soils these Downs samples are the least favorable for plant growth, being practically wholly lacking in humus (Fig. 27).

In the wooded kettleholes, in the Hither Woods, or in the Point Woods, the subsoil is very different. A glance at figure 28 shows, that on the average, the subsoils under the forest are higher in fine sand or silt than those under the grassland. In the case of the Hither Woods sample the soil is not far in its mechanical composition from the open Downs, and as the earlier description of that region has shown, the forest there is stunted. It is unquestionably the combination of this poor soil and exposure to the winds which holds back the growth of the oaks in the Hither Woods. How much this is retarded on the windward side of them has already been shown.

These different subsoils† appear to have an important influence in controlling the major distribution of the different vegetation types, always, of course, in conjunction with, and subsidiary to, climatic factors. Upon them depend the maintenance of the vegetative *status quo*. But the establishment and reproduction of either old or aggressively competing types must depend upon the upper layer of the soil, in which all alike must first root or germinate their seeds.

* For details of this see Fuller, M. L., The geology of Long Island, Prof. Paper U. S. Geological Survey 82: 1–231. 1914.

† In this, as in other parts of Long Island, my statements are based on many collections under each type of vegetation, so that the remarks about soil possibilities must be understood to refer to average conditions, rather than individual cases.

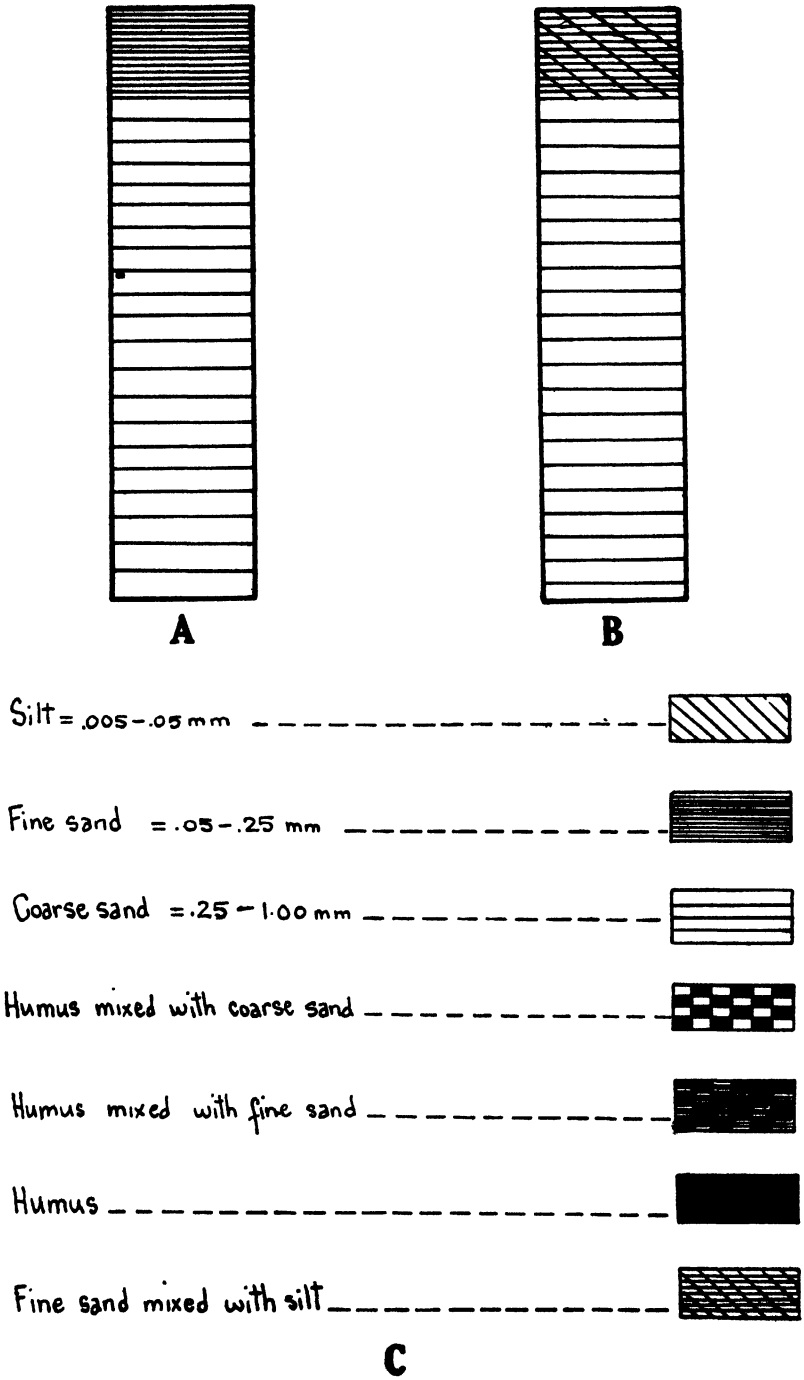


FIGURE 27. (a) Subsoil under open Downs at edge of Hither Woods; 15% fine yellow sand, 85% coarse yellow sand. (b) Subsoil under open Downs between Fort Pond and Great Pond; 16% fine sand and silt, 84% coarse sand. (c) Symbols used to designate size of soil particles in figures 27–30.

This upper layer, humus infested as it always must be, even in the worst sites, is the soil as it has been affected by the decomposition of successive generations of plants that have gone before,—again in the jargon of the gardeners, the topsoil.

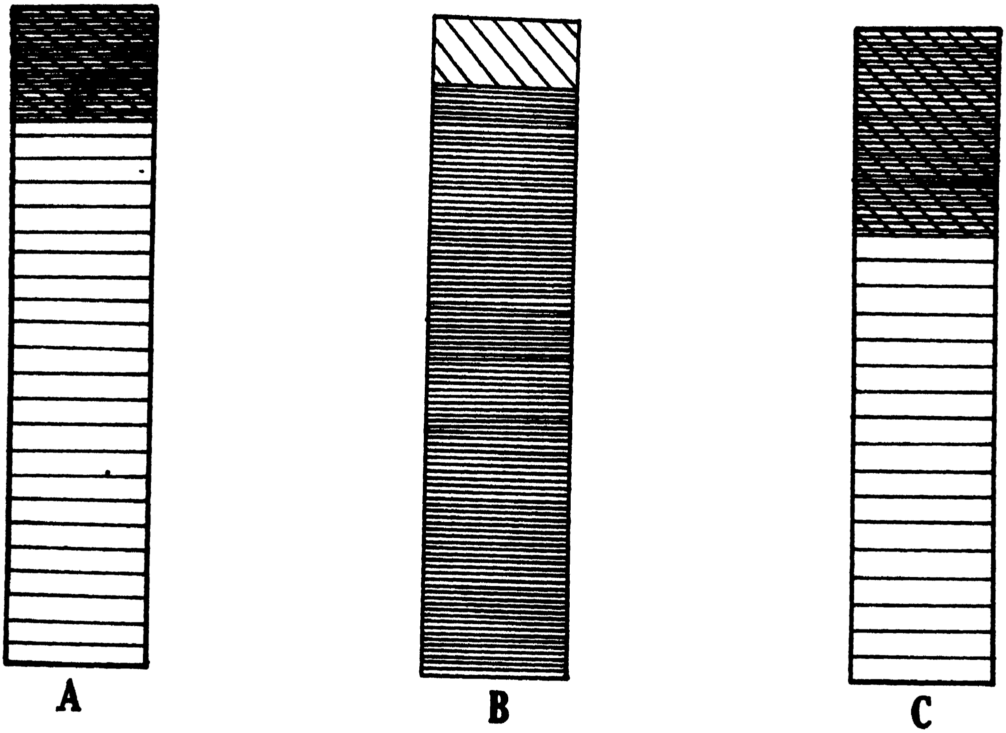


FIGURE 28. (a) Subsoil under the Hither Woods; 17% fine sand and silt, 83% coarse sand. (b) Subsoil under wooded kettlehole; 90% of fine sand, 10% silt. (c) Subsoil under Point Woods; 68% coarse light sand, 32% fine light yellow sand and silt.

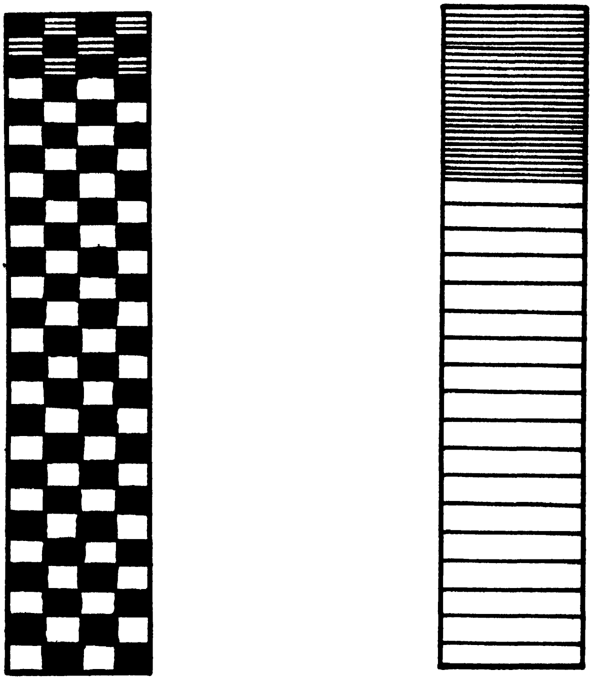
On the Downs this surface soil, often of varying thickness depending on the slope, is usually made up of much the same basic material as the mineral soil under it, but as Fig. 29 shows, with a pretty large proportion of humus in it. In the case of the surface soil under the woods, the same general proposition holds true, with the exception of the surface soil under the woods at Montauk Point. See figure 30.

These purely mechanical features of the soil are perhaps best measured, so far as their effects upon the vegetation are concerned, by the Hilgard*

* See Hilgard, E. W. Soils, Chapter IX, pp. 188-266, on "The Water of Soils," 1919. Also "The Wilting Coefficient for Different Plants and its Indirect Determination," by L. J. Briggs and H. L. Shantz, Bull. Bur. Plant Industry 230: 1-83. 1912.

method of determining the moisture holding capacity of them, and the Briggs and Shantz method of determining their wilting coefficient.

The moisture holding capacity of the subsoils of Montauk shows that, under the open Downs, they average 33.4%, while under the forest, averaging Hither Woods, Point Woods, the island in Great Pond, North Neck Woods, and wooded kettleholes, the figure is 39.9%. The interesting thing



A B

FIGURE 29. (a) Surface soil under open Downs near Hither Woods; 91% coarse sand and humus, 9% fine sand and humus. (b) Surface soil under open Downs between Fort Pond and Great Pond; 74% coarse sand, 26% fine sand, both darkened by humus, but not as much as in the sample from near the Hither Woods (a).

about these figures is that both of them are well above those for other regions of Long Island which sustain similar types of vegetation.

Taking the only other grasslands on Long Island we find the moisture holding capacity of their subsoils, as compared to Montauk, is as follows:

Hempstead Plains 28.9% Shinnecock Hills 26.5%

Montauk Downs 33.4%

The Montauk figure is not only considerably higher than any other grassland on the Island, it is even higher than the average of seventeen pitch pine subsoils over the rest of Long Island, the moisture holding capac-

ity of which is 31.6%. Considering the pitch pine type of vegetation as indicative of only slightly better conditions than the grasslands we are confronted with moisture holding capacity figures that are better than the average pitch pine soils, and yet a failure to produce this type of vegetation at Montauk.

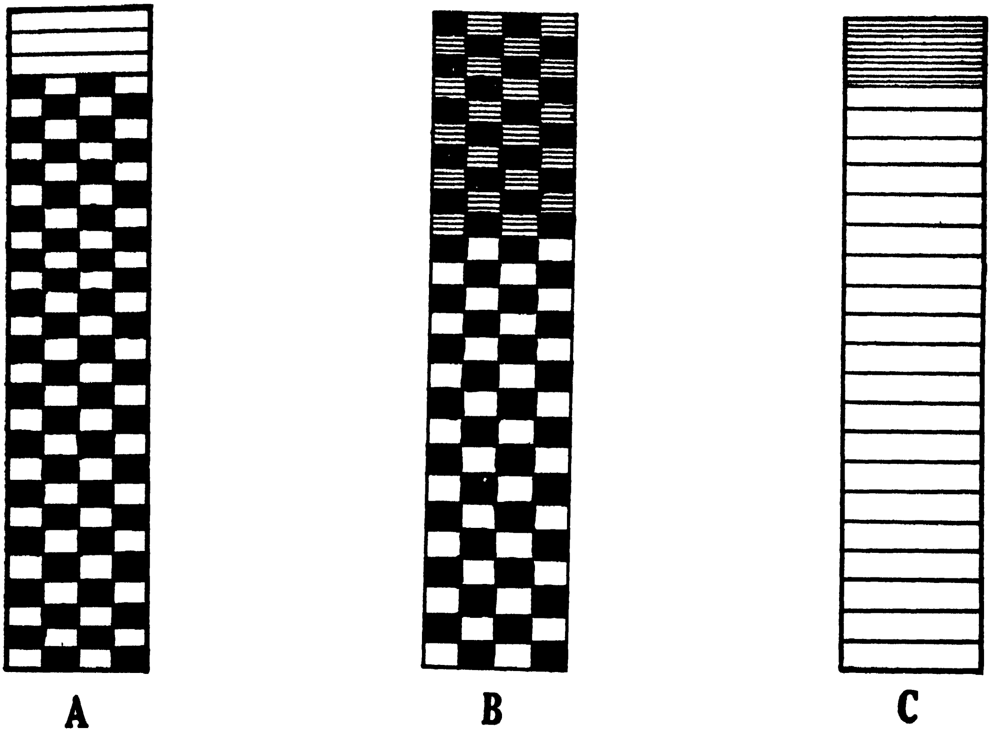


FIGURE 30. (a) Surface soil under Hither Woods; 90% humus and coarse sand, 10% coarse sand. (b) Surface soil under wooded kettlehole; 66% coarse sand and humus, 34% fine sand and humus. (c) Surface soil under Point Woods; 90% coarse sand, 10% fine sand, both only slightly darkened by humus.

In the case of the woodlands there is also a difference, as under eighteen different stations on Long Island, all supporting an oak forest, the moisture holding capacity of the subsoils averages 37.4%, while the figure for Montauk forest growth is 39.9%.

Both on the Downs, and in what woods occur at Montauk, there is thus a soil condition better than in other parts of Long Island, and, as we have seen, the failure to produce vegetation that might be expected to result from such conditions appears to be due to factors of climate already discussed.

Considering only the surface soils we have the following condition:

Grasslands	Moisture Holding Capacity
Montauk Downs	43.0%
Hempstead Plains	44.0
Shinnecock Hills	33.6
Forest	
Montauk	70.5%
17 Pitch Pine stations on L. I.	83.9
18 Oak stations on L. I.	97.2

The wilting coefficient of Montauk soils, is as follows:

Subsoils	Wilting Coefficient
Open Downs	4.7%
Forest	5.6
Surface soils	
Open Downs	6.1%
Forest	15.1

Other grasslands on Long Island average for the wilting coefficient of their surface soils 7.8%, which is close enough to the Montauk Downs to be of little significance. As might be expected, the *surface* soil, on grasslands, once that type of vegetation has become established, ought not to vary much from one place to another, for in every case we are recording not the capacity of the soil itself, but rather how that capacity has been affected by the vegetation which has captured it. That is why the wilting coefficient of the surface soils of all these Long Island grasslands is so nearly uniform.

While the fertility of Montauk soil is not known with any accuracy, one criterion of it is the vegetable garden near the Inn. This is about two acres, protected from most of the wind, and several years observation of it appears to indicate average fertility. Certainly the soil there is no worse than in hundreds of other gardens on eastern Long Island.

In attempting to see if the hydrogen-ion concentration of the soil has any effect on the vegetation many scores of tests according to the method of Wherry* have been made at Montauk.

Except for highly specialized habitats, such as cranberry bogs and salt marshes, the general uniformity of the specific acidity of these soils is noteworthy. From experience in making hundreds of these tests on other Long Island soils, as well as at Montauk, it may be safely stated that soils that range from a specific acidity of 3+ to 30+, or in most cases even to 100, are without significance, as to influencing the distribution of the major features of the vegetation. So far as individual *species*

* Wherry, E. T. Ecology **1**: 42–47, and 160–174. 1920. Rhodora **22**: 33–41. 1920. Amer. Fern. Jour. **10**: 15–22. 1920. Proc. Phil. Acad. Nat. Sci. **72**: 113–119. 1920. Smithson. Rep. **1920**: 247–268. 1922.

are concerned, there appear to be limits, but they are usually rather wide limits within which they prefer to grow. But even here the number of exceptions makes it hazardous to say that they will only grow in what appears to be their preferred habitat. And when it comes to whole vegetation types, the case is hopeless, as within each may be found an infinite variety of specific acidities, and nowhere that the writer has studied, any uniformity of it as to amount. Practically the only thing that may safely be said of the Montauk soils (excluding bogs and salt marshes) is that they vary in specific acidity from 3+ to 30+, and that this is without distributional significance, so far as the occurrence or extent of major vegetative covering is concerned Another factor which leads to accepting specific acidity with considerable caution as an active determinant in the distribution of vegetative types, is that it is a measure of what the decomposition of the plants has done to the soil, rather than a measure of the specific acidity of the soil *per se*. The tests for subsoils demonstrate this, as all over Long Island these vary only (with minor exceptions) from 3+ to 10. The surface soils, due to decomposition of the different types of vegetation supported by them, vary considerably, but as at Montauk, only within limits of little significance. In regions where there is a deeper accumulation of humus the variation is of course greater and of much more significance, as for instance, in the spruce forests in the north.

SUMMARY.

Montauk, which within historic times at least, has always been predominantly grassland, appears to be incapable of producing a forest, except under conditions of protection from the wind, and where there is available water. This, in spite of the fact that temperature, rainfall, humidity, evaporation and physical characteristics of the soil are as good as, or better than, those in the vicinity where forest growth is normal. The region is well within the general forest area of the northeastern states, and yet appears to be incapable of producing a forest, as that term is ordinarily understood. Of all the environmental factors, the wind is unquestionably the most important, and it may, upon subsequent experimentation, prove to be *the* factor.*

* It is a local tradition that trees will not grow on the exposed Downs. To test this twelve oaks (three each of four different species) were set out on the property of Guy DuVal, Esq., with different exposures to the wind. It is too early to report upon their condition, and as they are protected from fire and cattle, but not cultivated or watered, their response to their environment will be of interest. I am grateful to Mr. DuVal for this and for many other courtesies during numerous visits to Montauk.

While there is not much question that there have always been Downs and wooded kettleholes, and that the Hither Woods have always been about as they now are, there is at least some evidence that Montauk was once more thoroughly timbered than it has been since the first whites came there in 1640.

In 1849, J. A. Ayres wrote a book called "The Legends of Montauk," in which he says: "The limits of Montauk were once, perhaps, somewhat greater than they are at present. On the north side near the Great Pond are the *remains of a pine forest* which stood on ground now covered by the sea. The roots remain buried in the sand and are visible only on the receding of the tide." The writer has never seen these during the last ten years, and such evidence taken by itself would not be conclusive. But Elias Lewis, in his "Ups and Downs of the Long Island Coast"* says: "At Montauk Point, north of the lighthouse, is a low swampy place over which the tides sometimes rise. We are informed by Mr. J. F. Gould, who was for many years keeper of the lighthouse, that stumps are laid bare in front of this swamp, at the sea-margin, when the tide is extremely low." As hundreds of similar cases are known on Long Island, where what is now water or salt meadow was once forest, the Montauk records are, no doubt, simply local corroboration of a pretty common phenomenon. They all imply that the forest, and of course the island itself, was once more extensive than it now is.

That conception involves the proposition that the old coastal plain, marked roughly by the present 100 fathom contour, which is now far out to sea, supported a forest growth, which, through the submergence of this plain, was destroyed. The unquestioned occurrence of stumps of this now buried forest certainly supports this view.† At Block Island, Dr. Hollick postulates the destruction of the forest that remained after the submergence of this old coastal plain as due to man, but that, as the historical record indicates, could scarcely have happened at Montauk. But whether removed by the agency of man or the elements, the re-establishment of forest over Montauk or Block Island, without the protection, which the old coastal plain must have afforded, is practically impossible, except in locally protected places. Nor does it need much protection from these severe conditions to produce a forest, for at Gardiner's Island, only ten miles away, there is the finest deciduous forest growth on Long Island, if not in the whole of New York State.

* Pop Sci. Mo. **10**: 434–446. February 1877.

† See Hollick, A. Trans. N. Y. Acad. Sci. **16**: 9–18. 1898; Ann. N. Y. Acad. Sci. **11**: 55–72. 1898; Trans. N. Y. Acad. Sci. **12**: 189–202. 1893; Bull. N. Y. Bot. Gard. **2**: 392. 1902; and numerous papers by M. L. Fernald, who has adopted and greatly amplified the view of the effect of this old coastal plain on the distribution of species along the Atlantic coast.

PART II. FLORA OF MONTAUK.

It should be said at once that there has been no serious attempt to make collections of all the species that grow at Montauk, nor are introduced plants included here, unless they have entered into some of the vegetation types treated in Part I. But during many visits there, and in the course of a good deal of walking over the area, herbarium specimens were collected as they were necessary for the identification of species in certain associations of plants, or as their collection did not interfere with the study of the vegetation. It is from the accumulation of these notes and specimens that the following list has been made. While there can be no pretense that it is complete, it does at least show what species make up the great bulk of the flora of Montauk.

It is a pleasure to make acknowledgments to Mr. Kenneth K. Mackenzie for identification of the sedges; to Professor A. S. Hitchcock and Mrs. Agnes Chase for the grasses; to Dr. R. C. Benedict for the ferns and their allies; to Mr. W. W. Eggleston for *Crataegus;* to Mr. Paul C. Standley for *Vaccinium;* to Prof. E. S. Burgess for *Aster;* and to Dr. F. W. Pennell for certain Scrophulariaceae and for *Kneiffia.*

The names and specific identities, with a few trifling exceptions, are those in the writer's "Flora of the Vicinity of New York," which, in essentials, was based upon the "Illustrated Flora" of Dr. N. L. Britton and the late Addison Brown.

Practically all, except the records of the very commonest species, are supported by specimens. These are mostly in the herbarium of the Brooklyn Botanic Garden, while a few are in the collections at the New York Botanical Garden. Several score are based on specimens collected by Mr. William C. Ferguson of Hempstead, most of which he has presented to our collections. All other records are based upon field observations of the writer, or upon those of Mr. Ferguson. It is a genuine pleasure to acknowledge this assistance from Mr. Ferguson, who has also made many notes on the rarity or commoneŝs of certain grasses, sedges, and some other plants, which have been used in tabulations of the Raunkiaer "Growth-Forms," as these have been developed under the highly specialized conditions at Montauk.*

* The specimens collected at Montauk as well as many others from different parts of Long Island are all being studied with a view of getting out a "Flora of Long Island." The local Long Island collections of the Brooklyn Botanic Garden now number twenty

Explanatory Note.

The letters contained in the notes about the distribution of the different species mean the following:

V R = Very rare
R R = Rather rare
R = Rare
V C = Very common
R C = Rather common
C = Common

Usually where localities are cited it means that there is a specimen from that place, but, especially in the case of common plants, they are more widely distributed than the citation to the definite localities would appear to indicate. It is for this reason that the above plan has been adopted.

For place names see the map at the beginning of this book. As there defined "Montauk" means from the western end of Fort Pond to Great Pond; "Montauk Point" from the eastern edge of Great Pond to the Light house; and the "Hither Woods," as from the very earliest days, is applied to the forested tract west of Fort Pond.

Ferns and Fern Allies.

Ophioglossaceae

Botrychium obliquum. Woods at Oyster Pond; V R.

Osmundaceae

Osmunda Claytoniana. Wooded kettleholes; R C.
Osmunda cinnamomea. Kettleholes; thickets at Montauk Point; V C.
Osmunda regalis. Kettleholes. R C.

Polypodiaceae

Onoclea sensibilis. Kettleholes; Island in Great Pond; Montauk Point; R C
Dennstaedtia punctilobula. Kettleholes; Montauk Point; R C.
Dryopteris intermedia. Wooded kettleholes; R R.
Dryopteris noveboracensis. Wooded kettleholes; R C.
Dryopteris spinulosa. Kettleholes; Oyster Pond; R R.
Dryopteris Thelypteris. Kettleholes; V C.
Anchistea virginica. Kettleholes; R C.

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thousand specimens, not counting collections of the writer (about three thousand), the herbarium of Miss F. A. Mulford of Hempstead (about three thousand), several hundred specimens presented by Mr. Ferguson, an equal number of Lieut. Alexander Gershoy, and the herbarium of Miss A. E. Hamilton of Baldwin (1245 specimens).

Lorinseria areolata. Kettleholes; R.
Athyrium Filix-foemina. Wooded kettleholes; woods at Montauk Point; R R.
Athyrium thelypteroides. Open kettleholes; R C.
Pteridium aquilinum. Hither Woods; wooded kettleholes; Island in Great Pond; Point Woods; C.

EQUISETACEAE

Equisetum arvense. Waste places; C.

LYCOPODIACEAE

Lycopodium adpressum. Kettleholes; V R.
Lycopodium inundatum. Bog near Hither Woods; Montauk Point; V R.

Flowering Plants

PINACEAE

Pinus rigida. Dunes near Gin Beach; V R. Practically unknown except for a single wind-wrenched, stunted tree growing in pure sand, among *Ammophila*, *Lechea*, *Hudsonia*, and other dune species; but not very near the beach.
Juniperus virginiana. Edge of Hither Woods; Gin Beach; V R.

MONOCOTYLEDONES

TYPHACEAE

Typha angustifolia. Edge of Fort Pond; Island in Great Pond; R R.

SPARGANIACEAE

Sparganium americanum. Open Kettleholes; C.
Sparganium eurycarpum. Montauk Point; R R.
Sparganium lucidum. Oyster Pond; south end of Great Pond; R R.

ZANNICHELLIACEAE

Ruppia maritima. Oyster Pond; R C, but not found in many places.
Potamogeton dimorphus. Montauk Point; R R.
Potamogeton diversifolius. Ponds; R C.
Potamogeton Oakesianus. Kettleholes Montauk Point; Oyster Pond; R.
Potamogeton pectinatus. Ponds; R R.
Potamogeton perfoliatus. Reed Pond; Fort Pond; R C.
Potamogeton pulcher. Pond near Ditch Plain; R R.

ALISMACEAE

Alisma subcordatum. Open kettleholes; V C.
Sagittaria latifolia. Open kettleholes; V C.

ELODEACEAE

Vallisneria spiralis. Stream in Point Woods; Reed Pond; R R, but abundant where found.

POACEAE

Andropogon furcatus. Wide spread on the downs; C.

Schizachyrium scoparium. Dominant grass on the downs; V C.

Sorghastrum nutans. Downs and edge of Fort Pond; V C.

Paspalum psammophilum. Sand dunes; R R.

Paspalum setaceum. Downs near Hither Woods; R R.

Echinochloa Crus-galli. Open kettleholes; probably a relic of grazing. Introduced. R C.

Echinochloa Walteri. Oyster Pond; R R.

Panicum clandestinum. Open but high kettleholes near Culloden Point; R R.

Panicum columbianum. Downs; C.

Panicum Commonsianum. Downs; C.

Panicum depauperatum. Downs; V R.

Panicum dichotomiflorum. Oyster Pond; V R.

Panicum huachucae. Open downs; Hither Woods; R R.

Panicum implicatum. Thicket northwest of Inn; R.

Panicum meridionale. Hither Woods; open downs north of Inn; R R.

Panicum microcarpon. Oyster Pond, and edges of wooded kettleholes; R C.

Panicum Scribnerianum. Open downs; C.

Panicum sphaerocarpon. Downs; R C.

Panicum tennesseense. Wooded kettleholes; R R.

Panicum tsugetorum. Hither Woods; R C.

Panicum virgatum. Near Fort Pond and open kettleholes; R C.

Cenchrus carolinianus. Montauk Point; sand dunes; R R.

Anthoxanthum odoratum. Sparingly introduced; R R.

Aristida dichotoma. Culloden Point; R R.

Aristida purpurascens. Hither Woods; Downs; R.

Aristida tuberculosa. Beach; V R.

Cinna arundinacea. Oyster Pond; Reed Pond; C.

Agrostis alba. Freely introduced on the downs; Hither Woods; V C.

Agrostis maritima. Salt marshes; R R.

Agrostis perennans. Open stage of low kettlehole; C.

Ammophila arenaria. Dunes near Gin Beach; V C, but only at a few places.

Deschampsia flexuosa. Downs, and in Hither Woods; V C.

Danthonia spicata. Hither Woods; R.
Spartina Michauxiana. East of Inn; R.
Spartina patens. Fort Pond; V C, but only at a few places.
Spartina stricta. Fort Pond; R C.
Phragmites Phragmites. Island in Great Pond; V R.
Leptochloa fascicularis. Island in Great Pond; V R.
Eragrostis pectinacea. Downs; R R.
Poa pratensis. Downs; R R perhaps the result of grazing.
Poa triflora. V R.
Panicularia acutiflora. Kettleholes east of Inn; Montauk Point; R R.
Panicularia nervata. Wooded kettleholes north of Inn; R C.
Panicularia obtusa. Montauk Point; V R.
Panicularia pallida. Kettleholes; R R.
Elymus striatus. Oyster Pond; V R.

CYPERACEAE

Cyperus dentatus. Fort Pond and open kettleholes; Oyster Pond; C.
Cyperus diandrus. East side of Great Pond; R C.
Cyperus filicinus. East side of Great Pond; R C.
Cyperus filiculmis. Open downs; C.
Cyperus rivularis. Oyster Pond; V R.
Cyperus strigosus. Oyster Pond; V R.
Eleocharis acicularis. Fort Pond; V R.
Eleocharis Engelmanni. V R.
Eleocharis obtusa. Often the pioneer herb in low open kettleholes with seasonal ponds in them; V C.
Eleocharis palustris Oyster Pond; Fort Pond; R C.
Eleocharis tenuis. Open kettleholes; R C.
Eleocharis tuberculosa. Oyster Pond; R R.
Eriophorum virginicum. Bogs at Montauk Point; R R.
Scirpus americanus. Open kettleholes; Fort Pond; V C.
Scirpus cyperinus. Open and partly wooded kettleholes; V C.
Scirpus debilis. Oyster Pond; open kettleholes; R C.
Scirpus robustus. Gin Beach; R.
Scirpus validus. Swamp; R R.
Dulichium arundinaceum. Most moist places; V C.
Rynchospora alba. Oyster Pond; Great Pond; R C.
Rynchospora glomerata. Great Pond; Oyster Pond; Fort Pond; R C.
Mariscus mariscoides. Island in Great Pond; north of Inn; R C.
Carex alata. Open kettleholes; north of Inn; R R.

Carex albolutescens. Oyster Pond; Open kettleholes; R C.
Carex annectens. Kettlehole west of Inn; R R.
Carex blanda. Woods near Reed pond; R.
Carex canescens. East of Inn; R C.
Carex cephalantha. Near Culloden Point, on shore; Kettleholes east of Inn; R C.
Carex comosa. Wooded kettleholes northeast of Inn; R R.
Carex crinita. Near Oyster Pond; R.
Carex flexuosa. East of Great Pond; R.
Carex folliculata. Montauk Point; R C.
Carex hormathodes. Pool, Montauk Point; Oyster Pond. C.
Carex Howei. Open kettleholes near Ditch Plain; R.
Carex laevivaginata. R.
Carex lanuginosa. Near Culloden Point, on shore; north of Reed Pond; R.
Carex leptalea. East of Great Pond. R.
Carex lupulina. Kettleholes east of Inn; R R.
Carex lurida. Fort Pond; Reed Pond; C.
Carex Muhlenbergii. Downs; C.
Carex pennsylvanica. Hither Woods; R R.
Carex rosaeoides. Wooded kettleholes north of Inn; R.
Carex scoparia. Bog near Hither Woods; Open kettleholes; bog at Montauk Point; mostly as to the form *C. scoparia tessellata* Fernald; V C.
Carex silicea. Oyster Pond; Sea beaches; C.
Carex stipata. Near Oyster Pond; R R.
Carex Swanii. Near Oyster Pond; R R.
Carex vesicaria. Culloden Point, on shore; V R.
Carex vulpinoidea. Oyster Pond; V R.

ARACEAE

Arisaema triphyllum. Rich woods, Montauk Point; wooded kettleholes; R R.
Spathyema foetida. Low places in Point Woods; R R.
Acorus Calamus. Open kettleholes; Montauk Point; R R.

XYRIDACEAE

Xyris flexuosa. Low places; Montauk Point; R C.

ERIOCAULACEAE

Eriocaulon septangulare. Edge of Fort Pond; R R.

PONTEDERIACEAE

Pontederia cordata. Pool near Ditch Plain; R R.

JUNCACEAE

Juncus acuminatus. Oyster Pond; Open kettleholes; R C.
Juncus articulatus. Brackish marsh, Fort Pond; V R.
Juncus bufonius. Low places; V C.
Juncus canadensis. Most low places; V C.
Juncus dichotomus. Fort Pond; open kettleholes; V C.
Juncus effusus. Scattered in low kettleholes; R C.
Juncus Greenei. Downs; V C. Its tufts rather conspicuous on the open downs.
Juncus marginatus. Oyster Pond; kettleholes on Montauk Point; R R.
Juncoides campestre. Downs; R C.

MELANTHACEAE

Uvularia sessilifolia. Wooded kettleholes; Point Woods; C.

LILIACEAE

Lilium canadense. Oyster Pond; also near Fort Pond; R R.
Lilium philadelphicum. Oyster Pond; R R.
Lilium superbum. Along edges of ponds, marshes, Montauk Point; V R.

CONVALLARIACEAE

Vagnera racemosa. Island in Fort Pond; Montauk Point; R R.
Unifolium canadense. Point Woods; C.
Medeola virginiana. Point Woods; R C.

SMILACEAE

Smilax glauca. In thickets and kettleholes; V C.
Smilax herbacea. Oyster Pond; R R.
Smilax rotundifolia. In thickets and kettleholes; C.

AMARYLLIDACEAE

Hypoxis hirsuta. Point Woods; wooded kettleholes; R R.

IRIDACEAE

Iris prismatica. Meadows about Fort Pond; C.
Iris versicolor. Marsh near "Third House"; low kettleholes; R C.
Sisyrinchium arenicola. Downs; C.
Sisyrinchium atlanticum. Open kettleholes; C.

ORCHIDACEAE

Perularia flava. Old collection, not recently seen; V R.
Blephariglottis ciliaris. Fort Pond; R.
Blephariglottis lacera. Open downs; R R.

Blephariglottis psycodes. Reed Pond; V R.

Pogonia ophioglossoides. Most moist places; V C.

Arethusa bulbosa. Bogs at Montauk Point; V C, perhaps more so than at any other Long Island locality, except in the region north of Manorville.

Limodorum tuberosum. Bogs; V C.

Ibidium cernuum. Fort Pond; Montauk Point; R R.

Ibidium gracile. Downs; Montauk Point; R R.

DICOTYLEDONES

Salicaceae

Populus grandidentata. Thickets and in wooded kettleholes; R C.

Populus tremuloides. Near Fort Pond; R R.

Salix cordata. Edge of Great Pond; R.

Salix discolor. Kettleholes, and sometimes on Downs; north of Inn; R R.

Salix nigra. Fort Pond; R.

Salix sericea. Fort Pond; R.

Salix tristis. Downs Montauk Point; R R. Nothing like so plentiful as on other parts of Long Island, such as Hempstead Plains, for instance.

Myricaceae

Myrica carolinensis. Common on the Downs; V C.

Myrica Gale. Edge of Great Pond; R R.

Comptonia peregrina. Hither Woods; C.

Juglandaceae

Hicoria alba. Wooded kettleholes; R R.

Hicoria glabra. Hither Woods; Point Woods; R R.

Betulaceae

Carpinus caroliniana. Near Reed Pond; V R.

Corylus americana. Wooded kettleholes near Inn; Island in Great Pond; R R.

Betula populifolia. In some wooded kettleholes; often a pioneer in young thickets; C.

Alnus incana. Swamps in Point Woods; R R.

Alnus rugosa. Pool in Point Woods; R C.

Fagaceae

Fagus grandifolia. In wooded kettleholes; Hither Woods; North Neck Woods; R R.

Castanea dentata. Hither Woods, mostly dead; R C. Once a considerable element in the forest areas of the region.

Quercus alba. Hither woods; wooded kettleholes, and many other places; V C.

Quercus coccinea. In all wooded places on Montauk; V C.

Quercus rubra. Hither Woods; Island in Great Pond; R R.

Quercus velutina. Most wooded places on Montauk; C.

CANNABINACEAE

Humulus Lupulus. Island in Great Pond; V R.

URTICACEAE

Boehmeria cylindrica. Wooded kettleholes; R R.

Boehmeria Drummondiana. Near Fort Pond; V R.

POLYGONACEAE

Rumex Acetosella. Downs; V C. Introduced.

Rumex Britannica. Between Reed and Oyster Ponds; R.

Rumex crispus. Downs and along roadsides; C. Introduced.

Rumex persicarioides. Kettleholes; Great Pond; Oyster Pond; V R.

Rumex verticillatus. Oyster Pond; Reed Pond; R R.

Polygonum buxiforme. Fort Pond; Downs; Reed Pond; C.

Polygonum maritimum. Beaches; V R.

Polygonum neglectum. Beach near Oyster Pond; R.

Tovara virginiana. Oyster Pond; V R.

Persicaria hydropiperoides. Low open kettleholes; V C.

Persicaria pennsylvanica. Low open kettleholes; V C.

Persicaria punctata. Downs and open kettleholes; C.

Persicaria setacea. V R.

Tracaulon arifolium. Edge of Pool, Montauk Point; R C.

Tracaulon sagittatum. Kettleholes; R C.

Tiniaria scandens. Thickets; C.

Polygonella articulata. Downs; R C.

CHENOPODIACEAE

Chenopodium rubrum. Waste places and roadsides; V R.

Atriplex arenaria. Fort Pond; R.

Atriplex hastata. Beaches; R C.

AIZOACEAE

Sesuvium maritimum. Shores of Oyster Pond; V R. The only other stations for it known in New York State are at Easthampton and Gardiner'ssIland.

Alsinaceae

Cerastium arvense. Downs; C.
Arenaria caroliniana. Hither Woods; V R.
Moehringia lateriflora. Near Hither Woods, at contact of woods and downs; R R.
Honkenya peploides. Beaches; C.
Tissa marina. Fort Pond; R R.

Caryophyllaceae

Silene caroliniana. Near Fort Pond; R R.

Nymphaeaceae

Brasenia Schreberi. Pond near Ditch Plain; V R.
Castalia odorata. Most stable ponds; R C. The much smaller-flowered *C. odorata pumila* is also found with the type, and a pink-flowered form is not unknown.

Ceratophyllaceae

Ceratophyllum demersum. Ponds, Montauk Point; V R.

Ranunculaceae

Aquilegia canadensis. Point Woods; Hither Woods; R.
Anemone quinquefolia. Point Woods; R C.
Anemone virginiana. North Neck woods; V R.
Syndesmon thalictroides. Island in Great Pond; V R.
Ranunculus delphinifolius. Pool in wooded kettlehole near Gin Beach; V R.
Thalictrum revolutun. Point Woods; R R.

Lauraceae

Sassafras Sassafras. Hither Woods; Wooded kettleholes; Point Woods. R R.
Benzoin aestivale. Island in Great Pond; Point Woods; R R.

Cruciferae

Lepidium densiflorum. Shores of Gardiner's Bay; R R.
Cakile edentula. Sea beaches; R C.

Droseraceae

Drosera intermedia. Bogs; R R.
Drosera rotundifolia. Bogs; C.

Hamamelidaceae

Hamamelis virginiana. Point Woods; Island in Great Pond; R R.

ROSACEAE

Spiraea latifolia. Early wooded stage of open kettlehole; C.
Spiraea tomentosa. Southeast of Inn; R R.
Potentilla canadensis. Edges of woods; Downs; C. The form known as *P. pumila* is also found.
Potentilla monspeliensis. Downs; R R.
Argentina littoralis. Brackish marshes; C.
Fragaria virginiana. Point Woods; Wooded kettleholes; C.
Sanguisorba canadensis. Marshes; R C.
Geum canadense. Oyster Pond; R.
Rubus Chamaemorus. Between the Inn and Culloden Point; V R. See page 24.
Rubus flagellaris. Hither Woods; R R.
Rubus frondosus. Hither Woods; wooded kettleholes; R C.
Rubus hispidus. Wooded kettleholes; V C.
Rubus nigrobaccus. Kettleholes; Hither Woods; C.
Rubus procumbens. Scrambling all over the downs and through most thickets; V C.
Rosa carolina. Thickets; C.
Rosa palustris. Thickets; often on the downs; C.
Rosa virginiana. Thickets; V C.

MALACEAE

Aronia arbutifolia. Everywhere in low places; V C.
Aronia atropurpurea. In low places; C.
Aronia melanocarpa. Low places; V C.
Amelanchier canadensis. Wooded kettleholes; Hither Woods; Point Woods; C.
Amelanchier intermedia. Point Woods; R C.
Amelanchier nantucketensis. Hither Woods; wooded kettleholes; R R.
Crataegus albicans. Oyster Pond; V R.
Crataegus Arnoldiana. Montauk Point; V R.
Crataegus intricata. Point Woods; V R.
Crataegus Crus-galli. Near Culloden Point; R R.
Crataegus pruinosa. Wooded kettleholes, and Point Woods; R R.

AMYDGALACEAE

Padus virginiana. In most wooded kettleholes; Hither Woods; Montauk Point; C.
Prunus maritima. Beaches and many places in interior; V C:

CAESALPINIACEAE

Chamaecrista fasciculata. Downs; R R.

FABACEAE

Baptisia tinctoria. Downs; V C. See note on page 21.
Meibomia marylandica. Hither Woods; R R.
Meibomia obtusa. Gin Beach; Hither Woods; R R.
Lespedeza capitata. Downs; R C.
Lespedeza frutescens. Downs; C.
Lespedeza procumbens. Hither Woods; R R.
Lathyrus maritimus. Beaches; V C.
Strophostyles helvola. Thickets; R C.
Glycine Apios. Hither Woods; thickets; low open kettleholes; C.

GERANIACEAE

Geranium maculatum. Point Woods; Island in Great Pond; R R.

OXALIDACEAE

Xanthoxalis Brittoniae. Downs; R R.
Xanthoxalis cymosa. Downs; C.

LINACEAE

Cathartolinum intercursum. Downs; R R.
Cathartolinum medium. Downs; C.
Cathartolinum striatum. Low kettleholes; C.

POLYGALACEAE

Polygala cruciata. Low open kettleholes; Montauk Point; R C.
Polygala polygama. Downs; V C. The white-flowered form rather common.
Polygala viridescens. Downs; C.

EUPHORBIACEAE

Acalypha virginica. Edge of Hither Woods; R R.

CALLITRICHACEAE

Callitriche heterophylla. Montauk Point; V R.

ANACARDIACEAE

Rhus copallina. Wooded kettleholes; Hither Woods; V C.
Rhus glabra. Hither Woods and Point Woods; R R.
Rhus hirta. Hither Woods and Point Woods; V R.
Toxicodendron radicans. Nearly everywhere; V C.
Toxicodendron Vernix. Wooded kettleholes; V C.

Aquifoliaceae

Ilex opaca. Point Woods; Reed Pond; Hither Woods; R R.
Ilex verticillata. Wooded kettleholes; Point Woods; V C.

Aceraceae

Acer rubrum. In all wooded parts; V C. The form known as *A. caroliniunum* seems to be the only one at Montauk.

Balsaminaceae

Impatiens biflora. Wooded kettleholes; R R.

Vitaceae

Vitis aestivalis. Wooded kettleholes; C.
Vitis Labrusca. Wooded kettleholes; C.
Parthenocissus quinquefolia. Nearly everywhere; V C.

Tiliaceae

Tilia americana. Island in Fort Pond; V R.

Malvaceae

Hibiscus Moscheutos. Brackish marshes; V C. Pale and even white-flowered forms are also common.

Hypericaceae

Hypericum boreale. Low open kettleholes; V C.
Hypericum canadense. Thickets at Montauk Point; R R.
Hypericum majus. Oyster Pond; R R.
Hypericum mutilum. Downs; C.
Hypericum perforatum. Downs and in open kettleholes; V C. Introduced.
Hypericum punctatum. Downs and in open kettleholes. V C.
Sarothra gentianoides. Downs; V C.
Triadenum virginicum. Most low open places; V C.

Elatinaceae

Elatine americana. Kettleholes; V R.

Cistaceae

Crocanthemum canadense. Downs; Hither Woods; C.
Crocanthemum dumosum. Hither Woods; downs north of the Inn; R R.
Crocanthemum majus. Downs; C.
Hudsonia ericoides. Hither Woods; R R.
Hudsonia tomentosa. Beaches and sandy places; Downs; C.
Lechea maritima. Beaches and Downs; V C.
Lechea minor. Downs; Hither Woods; C.
Lechea villosa. Downs; C.

Violaceae

Viola cucullata. Point Woods, and some wooded kettleholes; R R.
Viola fimbriatula. Open downs; C.
Viola lanceolata. Low open kettleholes; V C.
Viola pallens. Point Woods; V R.

Cactaceae

Opuntia Opuntia. Near the Lighthouse; V R.

Lythraceae

Rotala ramosior. Kettleholes; V R.
Decodon verticillatus. In some low, nearly open kettleholes; C.

Melastomaceae

Rhexia virginica. Low open kettleholes; R C.

Onagraceae

Isnardia palustris. Low open kettleholes; C.
Ludwigia alternifolia. Low open kettleholes; C.
Epilobium coloratum. Oyster Pond; V R.
Epilobium lineare. Near North Neck Woods; Point Woods; V R.
Oenothera muricata. Downs; Low open kettleholes; beaches and sandy places; C.
Oenothera Oakesiana. Downs; Beaches and sandy places; C.
Kneiffia Allenii. Downs; C.
Kneiffia fruticosa. Kettleholes and open downs; V C. The forms to which the names *linearis* and *longipedicellata* have been applied, also occur at Montauk, but I have followed Dr. F. W. Pennell in considering them as mere forms of the type.
Kneiffiia pumila. Hither Plain; R.
Circaea lutetiana. Point Woods; Reed Pond; R R.

Haloragidaceae

Proserpinaca pectinata. Open kettleholes near Culloden Point; R C.
Proserpinaca palustris. Open kettleholes near Culloden Point; R C.
Myriophyllum humile. Pools; V R.

Araliaceae

Aralia nudicaulis. Hither Woods; Island in Great Pond; R C.

Ammiaceae

Hydrocotyle umbellata. Open kettlehole near Ditch Plain; Fort Pond; Great Pond; R C.

Sanicula canadensis. Oyster Pond; R R.
Sanicula gregaria. Reed Pond; R R.
Sanicula marylandica. North Neck Woods; R.
Cicuta maculata. Low, open kettleholes; C.
Deringa canadensis. In rich woods, Reed Pond; R R.
Sium cicutaefolium. Wet places; R C.
Ptilimnium capillaceum. Low open stage of kettleholes; V C.
Heracleum lanatum. Rich woods; Reed Pond; R R.

CORNACEAE

Cornus alternifolia. Island in Great Pond; V R.
Cornus Amomum. Oyster Pond; V R.
Cornus florida. Point Woods; R R.
Nyssa sylvatica. Most wooded kettleholes; V C.

CLETHRACEAE

Clethra alnifolia. In most wooded kettleholes; Montauk Point; V.C

PYROLACEAE

Pyrola elliptica. Island in Great Pond; Hither Woods; R.
Chimaphila maculata. Woods near Reed Pond; V R.

MONOTROPACEAE

Hypopitys insignata. Hither Woods; V R.

ERICACEAE

Azalea viscosa. All wooded kettleholes; V C.
Kalmia latifolia. Hither Woods; Point Woods; R C—at these two places, almost unknown elsewhere. At the Point Woods some of the specimens are the largest seen on Long Island.
Xolisma ligustrina. Wooded kettleholes; Point Woods; R R.
Epigaea repens. Hither Woods; Point Woods; R R.
Gaultheria procumbens. Most wooded places; R R.
Uva-ursi Uva-ursi. In Hither Woods, or along edges of them; R R. Not covering bare ground by the acre, as it does at Napeague or on Nantucket.

VACCINIACEAE

Gaylussacia baccata. Hither Woods and Point Woods, rare between; R C.
Vaccinium angustifolium. Hither Woods; Point Woods: R C.
Vaccinium atrococcum. Montauk Point; wooded kettleholes; R.
Vaccinium corymbosum. Nearly everywhere; V C.
Vaccinium vacillans. Hither Woods; R C.
Oxycoccus macrocarpus. Bogs, most common towards the Point; V C.

Primulaceae

Samolus floribundus. Island in Great Pond; V R.
Steironema lanceolatum. Thickets; low open kettleholes; R C.
Lysimachia quadrifolia. In woods; V C.
Lysimachia terrestris. Low open kettleholes; V C.
Trientalis borealis. Point Woods; Hither Woods; R C.

Gentianaceae

Bartonia virginica. Kettleholes; Downs; R C.

Apocynaceae

Apocynum cannabinum. Thickets; R R.
Apocynum pubescens. Thickets; R R.

Asclepiadaceae

Asclepias amplexicaulis. Hither Woods; R R.
Asclepias pulchra. Kettleholes; R C.
Asclepias syriaca. Thickets; C.
Asclepias tuberosa. Downs; R.

Convolvulaceae

Convolvulus repens. Low open kettleholes; R R.

Boraginaceae

Myosotis virginica. On the Downs; R C.

Verbenaceae

Verbena hastata. Thickets; R C.
Verbena urticifolia. Reed Pond; R R.

Lamiaceae

Teucrium littorale. Low open kettleholes; V C.
Trichostema dichotomum. Downs; Hither Woods; R C.
Scutellaria galericulata. Island in Fort Pond; V R.
Stachys hyssopifolia. Low open kettleholes; C. The form known as *S. atlantica*, and scarcely distinguishable from the type, is also found.
Stachys palustris. Montauk Point; R R.
Koellia incana. Downs; R R.
Koellia mutica. Downs; R R.
Lycopus americanus. Low open kettleholes; C.
Lycopus rubellus. Low places; R R.
Lycopus uniflorus. Low places; R R.
Lycopus virginicus. Low places; V C.

Mentha canadensis. Oyster Pond; R R.
Collinsonia canadensis. Reed Pond; V R.

SCROPHULARIACEAE

Linaria canadensis. Downs; R C.
Scrophularia leporella. In woods, and also in sand along north edge of Great Pond; Island in Great Pond; R R.
Chelone glabra. Swamps in Point Woods; R R.
Mimulus ringens. Oyster Pond; R R.
Gratiola aurea. Low open kettleholes; V. C.
Ilysanthes dubia. Low open kettleholes; R C.
Limosella aquatica. Oyster Pond; V R. The only known station on Long Island.
Agalinis acuta. Downs; V C.
Agalinis purpurea. Downs and low open kettleholes; R C.
Melampyrum lineare. Hither Woods; Point Woods; R R.
Pedicularis canadensis. Downs and along edges of woods; Montauk Point; R R.

LENTIBULARIACEAE

Utricularia macròrhiza. Pools; V R.

OROBANCHACEAE

Leptamnium virginianum. Hither Woods; Reed Pond; R R.

PHRYMACEAE

Phryma Leptostachya. Island in Great Pond; V R.

PLANTAGINACEAE

Plantago aristata. Downs; R R. Introduced.
Plantago major. Brackish marshes; R C. But only as to the form known as *P. halophila.*
Plantago maritima. Montauk Point; R R.

RUBIACEAE

Cephalanthus occidentalis. Low wooded kettleholes; V C.
Galium circaezans. Woods; R R.
Galium Claytoni. Low open and sometimes in wooded kettleholes; V C.
Galium pilosum. Low open kettleholes; Downs; C.
Galium tinctorium. Thickets; R R.

CAPRIFOLIACEAE

Sambucus canadensis. Low wooded kettleholes; Montauk Point; R C.
Viburnum dentatum. Low wooded kettleholes; R R.

Viburnum venosum. In most wooded places; V C.
Triosteum perfoliatum. On open downs near Inn; also Island in Great Pond; R R.

LOBELIACEAE

Lobelia inflata. Montauk Point; V R.

AMBROSIACEAE

Xanthium echinatum. Beaches; R C.

COMPOSITAE

Eupatorium hyssopifolium. Downs; C.
Eupatorium perfoliatum. Low open kettleholes; V C.
Eupatorium Torreyanum. Downs near Culloden Point; V R. Collected by William C. Ferguson, and reported by him also (Torreya **22**: 49. 1922) from Garden City and "Hempstead Plains."
Eupatorium trifoliatum. Thickets and woods; R R.
Eupatorium urticaefolium. Edge of woods, Reed Pond; R R.
Eupatorium verbenaefolium. Open and wooded kettleholes; R C.
Mikania scandens. Oyster Pond; V R.
Lacinaria scariosa. Downs near Hither Woods; R.
Chrysopsis falcata. Downs; V C.
Chrysopsis mariana. Downs; Hither Woods; C.
Solidago altissima. Island in Great Pond; Woods at Reed Pond; R.
Solidago bicolor. Hither Woods; Downs; R C.
Solidago caesia. Gin Beach; R R.
Solidago juncea. Downs; Montauk Point; R C.
Solidago neglecta. Bogs and low open kettleholes; V R.
Solidago nemoralis. Downs; C.
Solidago odora. Gin Beach; Reed Pond; R R.
Solidago rugosa. Thickets and kettleholes; V C. The plant known as *S. asperula* appears to be common with the type.
Solidago sempervirens. Brackish marshes and sand dunes; C.
Solidago serotina. Wooded kettleholes; R R.
Solidago speciosa. Montauk Point; V R.
Solidago ulmifolia. Montauk Point; V R.
Euthamia graminifolia. Open kettleholes; V C.
Euthamia tenuifolia. Open and wooded kettleholes; downs; Hither Woods; C. The form often called *E. minor* is also known.
Sericocarpus asteroides. Downs; Montauk Point; V C.
Aster cordifolius. Wooded kettleholes; C.

Aster divaricatus. Reed Pond; V R.
Aster dumosus. Downs; V C.
Aster ericoides. Open downs; Hither Woods; Point Woods; C.
Aster lateriflorus. Hither Woods; Reed Pond; R R.
Aster multiflorus. Wooded kettleholes; downs; C.
Aster novae-angliae. Near Prospect Hill; Reed Pond; R R.
Aster novi-belgii. Wooded and open kettleholes; R C. Also the forms known as *A. novi-belgii elodes* and *A. novi-belgii atlanticus.*
Aster paniculatus. Thickets; R R. Also as to form *simplex.*
Aster patens. Downs; Hither Woods; open kettleholes; C. Also well represented as to the form *A. phlogifolius.*
Aster puniceus. R R.
Aster spectabilis. Wooded kettleholes; R R.
Aster subulatus. Salt marshes; R R.
Aster tenuifolius. Salt marshes; R R.
Aster undulatus. Hither Woods; V R.
Aster vimineus. Thickets; V R.
Erigeron pulchellus. Low kettleholes; occasionally on the downs; R R.
Leptilon canadense. Downs; R C.
Ionactis linariifolius. Downs; V C.
Baccharis halimifolia. Salt marshes; R R.
Pluchea camphorata. Brackish marshes; R R.
Antennaria neodioica. Hither Plain; R R.
Antennaria plantaginifolia. Downs; V C.
Anaphalis margaritacea. Open kettleholes; downs; V C.
Gnaphalium uliginosum. Shore of Oyster Pond; V R.
Helianthus strumosus. Reed Pond; V R.
Echinacea pallida. Sparingly introduced on the downs; V R.
Coreopsis rosea. Low open kettleholes; R R.
Bidens connata. Low open kettleholes; R R.
Bidens discoidea. Low open kettleholes; R R.
Artemisia caudata. Beaches; R C.
Artemisia Stelleriana. Beaches; R C.
Erechtites hieracifolia. Kettleholes; downs; R C.
Cirsium discolor. Downs; R R.
Cirsium horridulum. Downs; R C. See page 21.

CICHORIACEAE

Cynthia virginica. Downs; V R.
Krigia virginica. Hither Woods; V R.

Lactuca sagittifolia. Gin Beach. V R.
Hieracium Gronovii. Downs; R C.
Hieracium marianum. Downs; C.
Hieracium scabrum. Downs; C.
Hieracium venosum. Downs and in dry wooded kettleholes; V C.
Nabalus serpentarius. Point Woods; R R.
Nabalus trifoliolatus. Hither Woods; Culloden Point; Montauk Point; R R.

The list enumerates 495 species contained in 261 genera which may be grouped as follows:

	Genera	Species
Ferns and fern allies	11	18
Gymnosperms	2	2
Angiosperms		
Monocotyledons	59	147
Dicotyledons	189	328
Totals	261	495

While these 495 species undoubtedly make up the great bulk of the flora of Montauk, 227 of them are either "common," "rather common" or "very common," and it is these elements which constitute the major features of the *vegetation* of the point. As shown elsewhere, and as a check of the foregoing list will verify, a trifle over 65 species are "very common" and it is these that give characteristic vegetative covering to great stretches of the Downs and wooded kettleholes.

Some years ago the Raunkiaer "growth-form" scheme of sorting species into different categories, according as they are suited to carry over their unfavorable season, was applied to the writer's "Flora of the Vicinity of New York," and to the 400 commonest species of the general flora of Long Island.*

At that time the opinion was expressed that the scheme did not satisfactorily indicate the response of either the total flora or of the four hundred commonest species of Long Island to the climate. It was hoped that in such a specialized region as Montauk the sorting would give us better results. The following table shows how far short Raunkiaer's scheme comes of reflecting the climatic conditions there. The percentages are as follows:

* Am. Jour. Bot. 2: 23-31. 1915. Mem. Brooklyn Bot. Gard. 1: 486-491. 1918. The details of Raunkiaer's growth-forms are given there, and will not be repeated here.

	MG	MS	MC	N	CH	H	G	HH	T
Normal Spectrum		6.	17.	20.	9.	27.	3.	1.	13.
Flora Vicinity of New York	.52	4.3	7.18	3.51	5.29	33.29	20.23	11.74	13.
Total Long Island flora	.89	4.37	6.34	2.77	5.89	33.15	20.10	10.90	13.94
400 common species of Long Island	1.50	3.	8.50	4.25	7.25	30.	21.	6.75	14.25
Total flora of Montauk		**1.6**	**11.4**	**3.1**	**6.9**	**32.6**	**19.2**	**11.2**	**13.5**
Commonest species of Montauk (including C., R.C., V.C.)		**2.2**	**10.1**	**5.7**	**6.1**	**30.3**	**19.3**	**11.4**	**14.5**

The significant thing about these percentages appears to be this: They agree pretty closely, except for the perfectly natural absence of tall trees, with those of the total flora of the Island, and this in spite of the fact that the climatic conditions of Montauk are very different from the rest of the Island. Assuming, as we must, that the age of the flora of Montauk is approximately that of the rest of the Island, we are faced with the proposition of a vegetative covering in marked contrast to Long Island generally, the components of which are simply the usual aggregation of Long Island *species*, but grouped in such very different percentages from the rest of the Island that the floral aspect of Montauk is unique. There are no endemic species there, and all but a handful of the rarest Montauk plants are found elsewhere on Long Island. This general agreement of the *flora* of Montauk with the rest of the Island, which the foregoing list of species will easily verify, is perhaps what is to be expected. But the failure of the growth-form percentages to reflect the very unusual sorting of these species-components of the Montauk vegetation, is perhaps the best local illustration of the failure of that scheme to reflect the response of plants to climate. As shown elsewhere in this account, that response has been rather definite, and has resulted in such a sorting of species that herbs vastly outnumber woody plants as *individuals*. And yet neither for the total Montauk flora nor for the chief species-components of its major vegetative features is there any but trifling indication in the Raunkiaer percentages of this response of the flora to the climate.

The absence of endemics there is perhaps of interest. Assuming again, as I think we must, that the flora of Montauk, with the rest of Long Island, began with what may, for the want of a better term, be called a definite capital or stock in trade of species, that capital has not, in the thousands of years that it has been subjected to the peculiar (for Long Island) conditions of Montauk, changed its components in sufficient amount to have produced endemic species. This comparative fixity of plant materials, it might even be called the immutability of Montauk species gives decided

color to the many arguments that species originate very slowly, even although conditions, apparently favorable for species segregation, such as the undoubtedly severe environment at Montauk, are at hand.* It may possibly be true also, that botanists who erect species concepts upon finer lines than the current manuals, would see in the dwarf, stunted or wind-wrenched specimens of the Montauk flora, a host of nascent species, in which the present writer sees merely ecological variations, or response to the local conditions there. A good illustration of this is the species that occur both in the wooded kettleholes and out on the open downs. Luxuriance in the one place and thwarted endeavor in the other to produce normal growth are constantly met with in the flora of Montauk.

The age of this flora,—it is, of course, all post-glacial,—cannot be fixed definitely. In an attempt to fix the relative age of different floras by the percentages of monocotyledons and dicotyledons,† Harper has shown that the former vary between 28% and 32.3% of the total flora in the glaciated region which he has studied. The percentage of monocotyledons at Montauk, also a glaciated region, but subject to invasion from the adjacent coastal plain, is 30.9%. Present ideas of the relative antiquity of monocotyledons may, however, put a different interpretation upon the proportion of them in any flora.

Another rather interesting feature of the plants of Montauk in relation to the environment is the so-called generic coefficient of the flora.‡ In brief this proposition is that in regions of diverse ecological conditions there will be a relatively higher proportion of genera produced than in a region of generally similar character. The plan has been tried for many regions and everywhere the generic coefficient (the proportion of genera to species in any given flora) is high where conditions are pretty uniform, lower where the conditions are diverse.

For the regions nearest Montauk, considering both introduced and native species the generic coefficients are as follows:

* This is in harmony with the statement of Professor M. L. Fernald at the recent meetings of the Botanical Society of America. In his paper "The Antiquity of species as indicated by Insular and Peninsular Floras of Eastern Canada" he postulates comparative fixity of species over long periods of years—25,000 years.

† Harper, R. M. A statistical method for comparing the age of different floras. Torreya **5**: 207–211. 1905.

‡ For an account of the details of this, first proposed by Professor Paul Jaccard, see Bull. Soc. Vaudoise Sci. Nat. **37**: 547–579. 1901. *loc. cit.* **44**: 223–270. 1908. New Phytologist **11**: 37–50. 1912. Rev. Gen. Bot. **26**: 1–47. 1914. Also a paper by Professor J. W. Harshberger on "The diversity of ecologic conditions and its influence on the richness of floras." Proc. Philadelphia Acad. Nat. Sci. **67**: 419–425. 1915.

	Generic coefficient
Flora of Long Island*	35.0
Flora of the Vicinity of New York	31.3
Connecticut Flora	31.9
New Jersey Pine-barrens	45.0
which should be contrasted with	
Montauk	52.6

Perhaps better than any other statistical method of studying a flora this Jaccardian generic coefficient reflects the uniformity of Montauk conditions and the effect upon the flora of that consistent topography and climate. As compared to the total flora of the vicinity of New York with 31.3%, and the Flora of Long Island with 35.0%, the 52.6% generic coefficient of Montauk is noteworthy as an expression by the flora of the relative ecological diversity of the larger areas, as compared to the relative uniformity of the smaller one.

* Based on the manuscript "Flora of Long Island," and doubtless not quite complete, but there is little evidence that additions will change the percentage more than a point or two.

FROM MONTAUK POINT.

I stand on some mighty eagle's beak,
Eastward the sea absorbing, viewing,
    (nothing but sea and sky),
The tossing waves, the foam, the ships in
    the distance,
The wild unrest, the snowy, curling caps—
    that inbound urge and urge of waves,
Seeking the shores forever.

Walt Whitman

BROOKLYN BOTANIC GARDEN

MEMOIRS

VOLUME III.

VEGETATION OF MOUNT DESERT ISLAND, MAINE, AND ITS ENVIRONMENT

By
BARRINGTON MOORE and NORMAN TAYLOR

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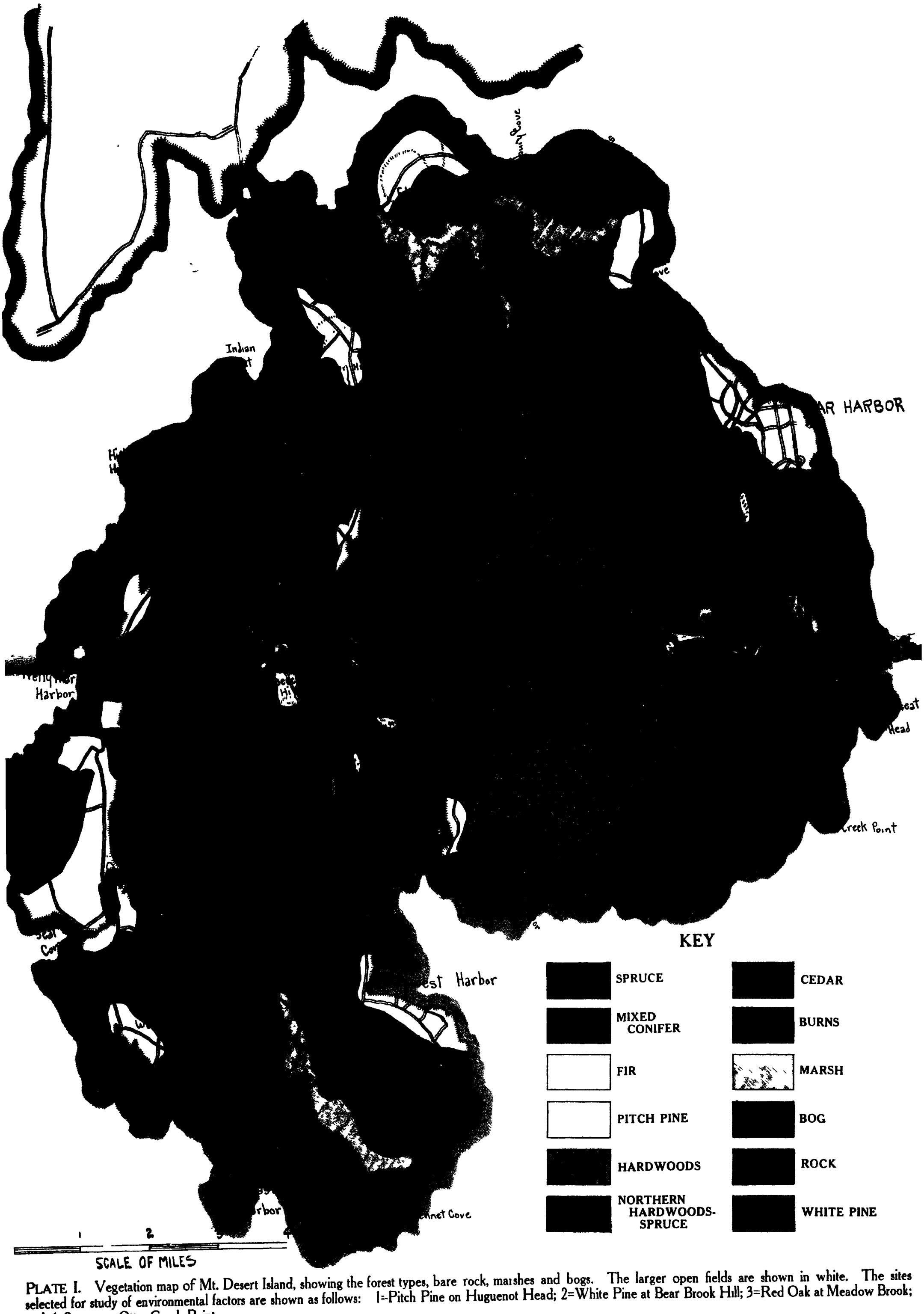

PLATE I. Vegetation map of Mt. Desert Island, showing the forest types, bare rock, marshes and bogs. The larger open fields are shown in white. The sites selected for study of environmental factors are shown as follows: 1=Pitch Pine on Huguenot Head; 2=White Pine at Bear Brook Hill; 3=Red Oak at Meadow Brook; and 4=Spruce at Otter Creek Point.

CONTENTS

VEGETATION OF MOUNT DESERT ISLAND, MAINE, AND ITS ENVIRONMENT

LOCATION

The island of Mount Desert is the largest and most beautiful of the many small islands lying off the coast of Maine. It is, however, not large for an island in salt water, and comprises an area of only about 100 square miles. Within this relatively small compass is a truly extraordinary assemblage of plant groups or associations. The island is a common meeting ground of plant associations which flourish from central New Jersey to Labrador. Many other places possess scattered plants which may be found elsewhere over large stretches of country. Mount Desert possesses not only interesting individual plants, but well-developed associations growing and reproducing themselves as living communities. These groups also pass through various stages of development from lower to higher forms.

The underlying causes permitting the existence of such markedly different groups in such close proximity to each other are of the highest scientific interest, and form the subject of our inquiry. We have endeavored to unravel as many of these causes as we might, in the hopes of adding a little to the meagre stock of knowledge concerning the requirements of some of the more important forest trees and other plants for moisture, warmth, light, and other factors on which plant life depends. Our concern is not with rare plants or botanical specimens, but with communities of plants acted upon by environmental forces, and in their turn reacting and modifying these forces.*

The present investigation may be considered as a first step toward the solution of the many varied and fascinating problems presented by the vegetation of Mt. Desert Island. We have endeavored merely to measure with simple instruments some of the climatic and soil factors, and to describe the vegetation, with particular reference to the different types of forest and the plants associated with each type, also to learn as far as possible the develop-

* In order to make the species concept and plant names used in this paper agree with some standard work, we have adopted those used in the seventh edition of Gray's Manual. This seems to us preferable, in a paper of no taxonomic significance, to adopting the many changes in both species and varieties which have appeared in *Rhodora* since the last edition of the Manual. We are under great obligation to Professor M. L. Fernald, Mr. K. K. Mackenzie, Dr. R. C. Benedict, and to the late Katherine Kimball for examining critical specimens.

mental trends or succession by which each type has arrived at its present stage and through which each must pass to reach what appear to be the highest types of forest which the island can produce under its present climate.

Fortunately, a considerable portion of the island, including all the important types of vegetation, as well as varied rock and land forms, from rugged mountains and cliffs to lakes, streams and basins, will be preserved for all time in natural condition within the boundaries of the Lafayette National Park. It should be mentioned in passing that the present study has not even scratched the surface of the opportunities afforded by this Park. Permanent plots should be established on which the vegetation would be carefully described, mapped and photographed; periodic observations would show trends of development that would be of the highest scientific interest and practical value.

LAND FORMS

The irregularity of the Maine shore line is due to the fact that it is a "drowned coast." The sea has invaded the land, making the hills into islands, and the valleys into bays. Take any map of hilly country on which the topography is shown by contours; select one of the contours, cover everything below it with blue crayon, leaving everything above untouched, and you will have the coast of Maine.

Mount Desert is famed for its bold mountains and cliffs, the highest mountains along the Atlantic Coast, reaching an elevation of 1532 feet only two miles from the sea. It has also the highest headland along the coast between Grand Manan and the Amazon. There are on the island 22 lakes and ponds, varying in size from an acre to 4 miles long by a mile wide. The ruggedness and variety of the land forms give a corresponding diversity of sites for plants of different requirements, and probably account in large measure for the richness of the plant and animal life.

Descriptions of country (physiography) will not be inflicted upon the reader except in so far as they are needed for an understanding of what follows. The principal feature is the series of bold granite mountains extending across the island in an east-northeast by west-southwest direction, and lying to the south of the middle in the widest part of the island. These, now more or less isolated, summits are part of a formerly continuous range which will be considered a little more fully below in speaking of the geology of the island. Their north slope is for the most part gentle, their south slope more abrupt. The east and west sides form precipitous cliffs overhanging the narrow passes between the now separate summits. These cliffs are important from the point of view of the plants as well as striking scenically.

This mountainous backbone, though intersected by numerous gaps, one of which—Somes Sound—is at sea level, nevertheless causes a noticeable difference between the climate of those parts of the island lying to the north and to the south of it. The fogs blanket the south side of the island and bank up against the mountains. Frequently the mountains suffice to hold the fog in check, and the north side of the island may be in bright sunshine while the south is bathed in fog. The difference between the amount of fog on the two sides of the island can not be stated exactly, but it must be considerable. The part of the island south of the barrier range is, therefore,

cooler and moister in summer than the part on the north. This topographic feature is important, and will be referred to again from time to time.

The country on both sides of the main barrier range varies from hilly to rolling. The flattest part of the island is the extensive southwest lobe. From each hill the view, when not shut off by the forest, is different from that obtained from every other hill. In some places one can easily imagine himself to be in the jagged mountains of the West. Most of the shore is bold and rocky. There is only one sand beach on the island and a small number of gravel beaches.

The five lakes of considerable size all either lie or head in the main mountain barrier, their beds evidently having been scooped out by the glacier from smaller stream valleys. The other lakes and ponds are scattered, principally on the north side of the island.

There are a number of marshes (some salt), swamps and bogs, all of which afford habitats for interesting plants.

GEOLOGY

The geology is considered only so far as it affects the vegetation. We do not know the age, or geological horizon as it is called, of a single one of the rocks of Mt. Desert Island. Such distinguished geologists as N. S. Shaler and W. M. Davis have studied the geology to a limited extent, and it is from their work that the following brief account, except that of the period following the glaciers, is taken.

The rock which seems to be the oldest is a greenish sedimentary, long since crushed by the pressure of overlying rocks into a schist. Apparently, thick layers were deposited on this, then worn away before the next series of rocks was laid down. This green schist crops out on the west side of the island, and has been named the Bartlett series after a neighboring island on which it is prominent. The next oldest rock, probably eons younger than the schist, but still millions of years old, is a series of slates, sandstones and flagstones, well seen at Bar Harbor near the steamboat landing, at Northeast Harbor and other places. Then there are, at the Ovens, on the southwestern extension of the island and elsewhere, exposures of light colored ancient lava-flows known as felsites. There are also evidences of eruptive movements. These lavas appear to be contemporaneous with the sedimentary slates and sandstones above mentioned. Then came intrusions of a dark colored igneous crystalline rock known as diorite, consisting chiefly of hornblende and triclinic feldspar.

The geological process which, though but one of many profound changes undergone by the region, has left its imprint most strongly today, is the thrusting of great masses of molten granite into the overlying rocks. The coarse crystalline texture of the granite, even on the highest summit, shows that this rock cooled far below the surface. Thus we must picture the present granite mountains as the roots or remnants of older lofty mountains possibly as high as the Alps.

The only rocks now recognized as later than the granite are the dark colored trap dikes which cut through all the other rocks of the island, even the granite, in one place or another. These are conspicuous and readily recognized. Nowhere is there any indication of overflow. If they reached the surface, it was far above that of today; thus they afford additional evidence of the vastly higher mountains, of which we now see the wasted remains. An important feature of these dikes is that they are said to contain small amounts of lime, though in a form difficult for plants to obtain.

After being worn down by the end of late Cretaceous time to nearly a plain, or peneplain, out of which the more resistant rock masses stood as isolated hills or monadnocks, the land was again uplifted to a moderate extent. The valleys of today, aside from modification by glacial action, have been cut down since this uplift.

The foregoing gives a brief outline of the rocky base or framework of the island. The form which we see today is the result of severe glaciation acting upon this rocky base. Let us not forget that what we see is but one of the unnumbered stages through which the region has passed, and will pass; a mere drop in the vast ocean of geological time.

The thickness of the ice sheet during the last glacial period is unknown, but it lay above the present summits. The direction of movement was east of south. The less resistant places in the granite, perhaps where dikes were more numerous, were cut into by the ice of the different glacial periods until no less than nine great gaps were formed, some of them extending deeper than the present sea level. How much of this cutting was done during the last glaciation, and how much during earlier periods, it is impossible to say. These ice-formed passes have changed the single granite range into a series of long mountains each running at right angles to the course of the range, or west of north by east of south. The steep east and west sides of the mountains, noted above, are probably due to the increased cutting power of the glaciers on being forced into the passes. The magnitude of this power is reflected in the depth to which the ice has cut; in some of the gaps the deepest portion is in the narrowest place between the steepest cliffs.

The south-facing slopes are steeper than those facing to the north. This is to be expected from the action of the ice sheet which, in overriding a mountain mass, exerts a "plucking" effect on the far, or south, side as it passes on. Shaler (1889) believed that these south faces are steeper than would be accounted for by the ice alone, and attributes the series of cliffs and benches which are such a conspicuous feature of these slopes to cutting by the waves of the sea. He considered that the island was submerged "certainly to the height of 1300 feet" and probably to the summit of its highest mountain since the retreat of the ice. He based his theory on three lines of evidence: the similarity between the benches on the south slopes, where the waves would have a chance to cut, and the scarps and benches found along the shore today; chasms apparently formed by the pounding of the waves in the weaker portions of the rock; and the absence of a mantle of till, which is always deposited by the ice, from even the gentler sloping rock to the very summits. Nevertheless, geologists today are practically unanimous in the belief that no such submergence as Shaler postulated has occurred since the last retreat

of the ice. All agree that there was a submergence, but its maximum seems to have been about 210 feet (de Geer, 1892). The evidence of wave action along the Cadillac Cliffs west of Thunder Hole at approximately 200 to 220

FIG. 1. Rock-bound shore of Mt. Desert Island. Otter Cliffs, showing wind-swept spruce. The low vegetation on top of cliff is the arctic alpine crowberry (*Empetrum nigrum*), which inland grows above timber line. This is the most northerly vegetation on the island, owing to its proximity to the cold waters of the Gulf of Maine.

feet is very strong. Perhaps the subsidence which Shaler thought took place after the last retreat of the ice may have occurred in the last interglacial period, before the last glaciation. Along the Beechcroft path up Huguenot Head (Pickett Mountain), there is a very distinct horizontal glacial gouge along the face of one cliff which would be a sea cliff according to Shaler's theory. Obviously the ice sheet passed along here *after* the cliff had been formed. The lack of a mantle of till might be due to the fact that the deposit on the smoothed granite surface of the upper slopes of the mountains was thin, and has been washed away by the rains of fifteen or twenty thousand years since the ice retreated.

We come now to a portion of the geological history of the island which profoundly influenced the make-up of the vegetation which we find today. The evidence appears to point conclusively to a former extension of the coastal plain from its present termination at Cape Cod as far as Newfoundland. Fernald (1911) shows that beyond a reasonable doubt such a land connection affords the only possible explanation of the presence of the coastal plain plants now found on Newfoundland, in the face of the absence of common plants from the Gaspé Peninsula which could much more easily be transported to Newfoundland by birds, wind, floating ice and logs, or ocean currents.*

We need not repeat the details which Fernald has set forth as the basis for the existence of this land bridge. For our purpose it will be sufficient to outline the events which the evidence indicates probably occurred. It is well known that the coastal plain which borders our Atlantic Coast extends out under the ocean for a good many miles to what is known as the edge of the continental shelf. At the 100 fathom line, which is taken as the edge of the continental shelf and outer border of the submerged portion of the coastal plain, there is a steep drop to the main bed of the Atlantic Ocean. From Texas to the Hudson River a considerable portion of the coastal plain is above the sea, comprising the extensive level stretches between the Piedmont hills and the ocean. East of the Hudson River an increasing portion of the coastal plain is submerged, until it ends as dry land at Cape Cod. Long Island, and the islands to the eastward, with Marthas Vineyard and Nantucket, were formerly parts of this plain. But, though under water, its eastward continuation can readily be traced by soundings where it forms the shallow water off the Gulf of Maine east of Cape Cod known as Georges Bank as well as Brown Bank still farther east. It reappears as land again

* See Fernald, 1911, especially pp. 135–162, on "The Geographic Origin of the Flora of Newfoundland." His facts and conclusions apply equally well to some of the plants of Mt. Desert Island.

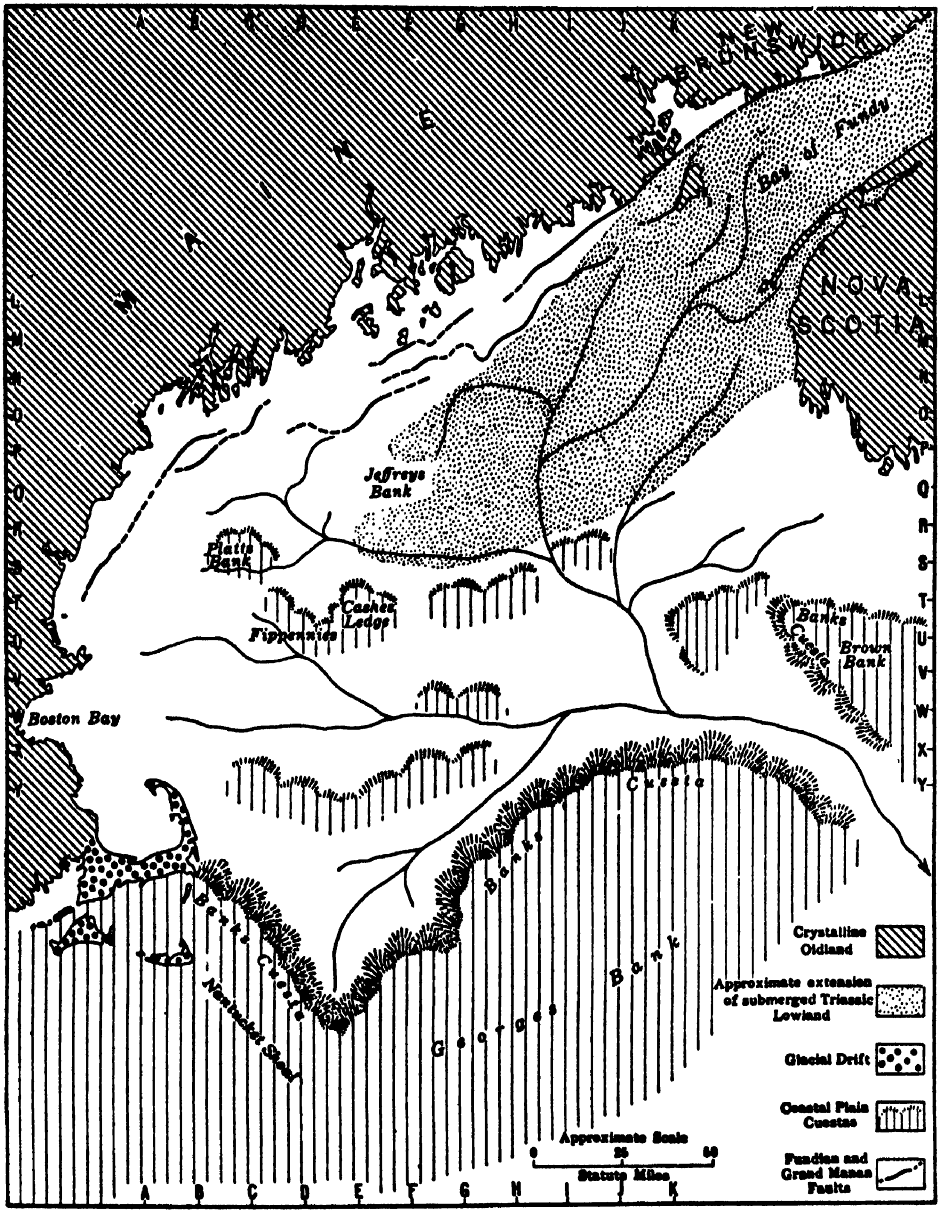

FIG. 2. Sketch map of the floor of the Gulf of Maine and the adjacent Banks comprising the former coastal plain, now submerged. This shows the Banks Cuesta, hypothetical pre-glacial drainage of the lowland, and the submarine scarps of the Fundian Fault. After D. W. Johnson.

in Sable Island off Nova Scotia. In places it is only barely submerged, as little as 2 fathoms at Georges Shoal. An elevation of only 20 fathoms in the sea bottom would here uncover a considerable area of land. An elevation of 100 fathoms would bring above water the large area off our eastern coast extending out to the continental shelf. Since this eastward and northward continuation of the coastal plain in former times is of the utmost importance in accounting for the occurrence of certain coastal plain plants on Mt. Desert Island, especially the scrub oak, which is heavy seeded and could not be transported by winds, animals, currents and so forth, the map given by Johnson (1925, page 295), is here reproduced as figure 2.

Johnson and Stolfus (1924) have projected a series of 25 profiles north and south across the Gulf of Maine. They find that Georges and Brown Banks have the typical form of a cuesta (low ridge) analogous to that in the coastal plain of New Jersey with a gentle slope toward the southeast and a steep inface toward the deeply submerged inner lowland. The lowland floor is trenched by what appear to be normal river valleys. They say "in this drowned inner lowland we find convincing evidence of a geologically recent submergence exceeding 1200 feet." Recognizing the important bearing of a geologically recent stand of the land 1200 feet higher than now, for a considerable period of time, on certain problems of plant distribution, they discuss Fernald's hypothesis of a land connection between the Pine Barrens of New Jersey and Newfoundland. They mention Barrell's view that migration after the last glacial epoch would have had to take place during a cold period, while it appears more probable that such a migration must have occurred while the climate was as warm as that of the present, or warmer. "The submarine physiography of the Gulf of Maine indicates that . . . instead of a temporary land bridge due to bulging at the margin of the glacier, we apparently had relatively permanent normal coastal plain conditions continuously from New Jersey to Newfoundland. It seems most probable that the plant migration took place prior to the ice advance, when conditions for such migration apparently were most perfect and most long enduring; and that the remnants of the flora survived that ordeal on favored parts of the coastal plain." In response to an enquiry as to whether there is anything in the botanical evidence as known today to negative such a migration in preglacial time they quote Fernald as follows: "There is absolutely no botanical reason, so far as I can see, why this might not have been the case. In fact, there are certain rather striking points which would indicate that a migration in late Tertiary or early Pleistocene times took place."

It is not unlikely that, as the ice advanced, the coastal plain plants retreated to the edge of the wide coastal plain which was not reached by the

southernmost extension of the ice sheet. With the final retreat of the ice, these plants reached the mainland, where they are found today.

It is possible that the extension of the coastal plain from Long Island to Newfoundland, or a considerable portion of it, existed above the sea after the last retreat of the ice. The shallowness of parts of Georges and Brown Banks has already been mentioned. The loose, unconsolidated materials of the coastal plain, with no rock to resist wave action, are rapidly cut away. Fernald emphasizes this fact, and cites figures to show the marked decrease in the size of Sable Island, even in historic times. The action of the waves on Long Island is such that at Montauk Point the bluffs are constantly being worn away. Therefore, it is not at all unlikely that considerable areas of land, bearing coastal plain plants, existed in comparatively recent times where now we find the shallow waters of the various Banks.

SOIL

The various properties of the soils in relation to the vegetation, so far as we were able to study them with the simple methods available, will be found below in the section on THE ENVIRONMENT, on pages 47–58. We are here concerned only with the general features.

There has never been a soil survey of Mt. Desert Island. The soils of the island were deposited by the ice sheet during the last glacial period, or, in some places below 200 feet elevation, by marine action during submergence following the retreat of the ice. Some of the soils below 200 feet, though not deposited by the sea, have been reworked by the waves. Large areas on the mountain slopes are bare of soil altogether, except for occasional shallow pockets of glacial till, a little coarse material from the weathered granite, and here and there an accumulation of acid humus from the vegetation in places which have escaped fire for long periods. Bare, or nearly bare, rock is, however, not confined to the mountain slopes. Rock ledges of varying size are common on the more level parts of the island, possibly on account of the washing away of the mantle of till by the waves. Some of these ledges are practically bare of soil, others have a little disintegrated rock and humus. Still others are so covered with a mat of humus in which the forest has become established as to be almost indistinguishable from the neighboring areas of soil, except for the poor growth of the trees.

There are three main classes of soil on the island, a reddish brown to yellow glacial till with varying amounts of stones, a sand with varying proportions of gravel, and a fine grey or bluish silt or clay of marine origin. The glacial till is by far the most widespread soil, covering more than three-quarters of the island, not considering bare rock. It is mostly a reddish brown stony loam with a fair proportion, about 10 to 20 per cent, of finely divided material, but not much clay, as indicated by the fairly rapid settling, leaving only a slight cloudiness. Some parts are, however, yellowish brown. There are places where the clay content reaches a higher proportion, though not enough to make the soil heavy. This reddish brown till, when newly dug up from the forest and unmixed with humus, has been found very infertile. Experiments with coniferous seedlings and corn showed very poor growth, both of root and tops (Moore, 1917). This is not due to acidity, since tests by the Wherry (1920) method showed specific acidities of only from 3 to 30 (pH 6.5 to 5.5) though in some places it ran as high as 100 (pH 5.0).

It may be accounted for by the high amount of iron, which gives the reddish color, by the presence of a toxic substance, or by the unavailability of the nutrient materials on account of the comparative newness of the soil. Where this soil is in contact with the blanket of "duff," or raw humus, it has been leached to an ashy grey color by the removal of the iron. This grey soil, sometimes known as "podsol," forms only a thin layer, an inch to a few inches in thickness, and is generally rather acid, from 30 to 100 (pH 5.5 to 5.0) on the Wherry scale.

The pockets of sand and gravel are not large or numerous, but are important owing to the high proportion of white pine in the forests growing on them. The soil where examined is a light yellow rather fine sand with a high proportion of water-rounded stones, and may possibly be wave-washed glacial till instead of a true sand deposit. But there are also small pockets of unmistakable water-laid sand in which cross bedding is plainly seen.

One of the most interesting types of soil is the fine clay and silt. There appear to be two kinds, a blue marl or true marine clay containing marine shells, and a very fine silt. The former occurs only here and there in pockets. The latter is rather widely distributed below the 200 foot level where the form of the land permitted quiet water during the submergence which followed the retreat of the ice sheet. One of the largest examples is the extensive meadow east of the high cliffs on Champlain (Newport) Mountain. Evidently Cranberry hill, though low, was sufficient to form a sheltered lagoon which silted up. The resulting soil is heavy and looks at first sight like a clay. In reality it is a fine grey silt without much clay, as indicated by fairly rapid settling. It is poorly drained and poorly aerated, and where the forest cover has been removed, becomes hard and cracked when dry, and pasty when wet. Under the forest, when mixed with humus, it appears to be fairly fertile, but when cleared it seems to be difficult to work. Its reaction is neutral.

It is not uncommon, especially on the northern side of the island, to find a blue clay probably of glacial origin, generally overlain by the usual reddish brown glacial till. Further studies of these deposits might throw light on the occurrence of different periods of glaciation.

POST-GLACIAL MIGRATION OF VEGETATION

In order to understand why certain plants are found on Mt. Desert Island today it is necessary to consider not only the existing environment, that is, the character of the climate and soil, but also the history of the region since it was laid bare after the retreat of the ice. Plants migrate just as human beings do, extending into new regions in which they find conditions suitable for their establishment and growth. These migrations have been going on since glacial times, and may be continuing—slowly and imperceptibly—today. Theoretically they would cease only when climatic conditions had remained stable long enough for each plant to spread out into all the accessible lands where it could grow successfully in competition with the other plants of the same locality. Such a condition requires long periods of time, thousands of years. Since it is doubtful if conditions have been as they are today for a sufficient length of time to bring about a state of equilibrium, it is reasonable to suppose that the northward migration which followed the retreat of the ice still continues. Obviously, this is a difficult matter to determine, particularly in view of the disturbances to which the plants have been subjected since the advent of the white man. But indications point in that direction (Adams and others, 1920, see especially p. 285).

At the maximum extension of the ice of the last glaciation, the vegetation along the front of the ice sheet must have been composed of boreal plants. Just how far south of the ice this northern flora spread we do not know. But it is now thought that possibly the influence of the cold did not reach out as far beyond the ice as used to be supposed. If this be true, then the zone of boreal plants between the ice and the mild climate vegetation must have been comparatively narrow, much narrower than the area of the corresponding vegetation today.

As the ice slowly retreated (Antevs, 1922) the ground laid bare was occupied by a boreal type of vegetation, forests of spruce and fir, and bogs of arctic plants.* The cover formed by these forests is ordinarily so dense that it must have kept out the invaders from farther south, even when the climate had become better suited to their growth. But eventually the southern

* The rate of retreat in cent. l New England has been measured by Antevs, employing Baron de Geer's method of counting the annual layers in clay deposits. He found that from Hartford, Conn., to St. Johnsbury, Vt., a distance of 180 miles, the time required was 4000 years, during which the rate was not, of course, uniform.

forms crept in, gaining a foot-hold, at first on the rockier and more open places, and later spreading into the gaps in the forest as opportunity offered.

It has already been shown that before the glacial period the coastal plain extended from Cape Cod to Newfoundland, and must have borne plants which now occur in eastern New Jersey. Just when submergence took place is not known, but it is reasonable to suppose that parts at least of the coastal plain were above the water during and perhaps shortly after the last glaciation. The climate of this vanished portion of the coastal plain, except during the glacial periods, must have resembled that which now prevails on Cape Cod and Long Island rather than that of the present coast of Maine. The cool summer climate, which attracts so many people to the Maine Coast, is due to the cold waters of the Gulf of Maine, not to a southward extension of the Arctic current, as was formerly supposed. This coldness results mostly from the low winter temperature of the land mass adjacent to the Gulf of Maine (Bigelow, 1914 and 1922). The storms and cold "waves" of the winter travel from west to east, passing from the land out over the sea. When the coastal plain was dry land there was no Gulf of Maine to receive the winter cold and store it on into the summer. The lakes or sounds which then existed must have had very little effect indeed, compared with the present large mass of water. Therefore, other things being equal, the land now along the shore, then at a considerable distance inland, would be warmer than it is now.

The coastal plain must have borne considerable areas of pitch pine and other southerly plants before it disappeared beneath the waves. As the subsidence and wearing away progressed, the plants were driven back until they reached the older land which bordered the coastal plain. Some species may have perished in the retreat, but a considerable number managed to establish themselves on the older land. There, on situations suited to their requirements, they today form groups in which one may, as he looks around, readily imagine he has been suddenly transported to coastal New Jersey. Surely, if we may be permitted to imagine that some unknown force had exterminated the coastal plain plants from the entire coast of Maine, it is difficult to believe that they would ever become re-established under present conditions, except for those species which are disseminated by birds, and possibly also those spread by winds. In other words, they reached Mt. Desert Island under a set of conditions which no longer exists. Once there, they have been able to maintain themselves, chiefly in the rockier and more open places.

Of the more northerly plants which followed the retreat of the ice, a few still remain. A conspicuous example is the crowberry, *Empetrum nigrum*, which is abundant along the shore cliffs, but inland is found only above timber

line and in bogs where it has been left as a relic of the former cold which prevailed near the retreating ice front. The trees which formed the earlier post-glacial forests, the black spruce, *Picea mariana,* white spruce, *Picea canadensis,* fir, *Abies balsamea,* red spruce, *Picea rubra,* with possibly the paper birch, *Betula alba papyrifera,* are found on the island today. The red spruce is probably the most abundant tree. The earlier forests were probably largely black spruce, stunted and slow of growth, followed by white spruce. Today, the black spruce is confined to the bogs, in which some of the plants probably represent fairly well those which grew in the surrounding country just after the withdrawal of the ice sheet. The white spruce is still abundant, particularly along the margin of the island near the cold sea water, where it sometimes outnumbers the red spruce. Thus it may be seen that the glacial period has left many evidences, not alone on the rocks and soil, but on the present vegetation of the island.

HISTORY

Because the actions of man, red and white, since the occupation of the island, have materially affected its vegetation, we could wish that the record were more complete. How long the Indians lived on the island before the white man came, we have no means of knowing. But it is evident that with their crude culture and stone implements they would be able to effect less change in a thousand years than the white man could in ten. The Indians had, nevertheless, one means of destruction in common with the white man—fire. We know that in hunting they sometimes set fires in order to drive out the game (Street, 1905, p. 60). This seems to have been a common practice among all Indians who depended largely or wholly on hunting. Yet there were still vast stretches of magnificent timber when the white man came. Possibly the fires were comparatively small. It is also more than probable that the fires burned with less fierceness before the forests were cut. The destructive fires of today which so frequently follow logging operations often start in the fallen tops and other debris. Furthermore, an untouched forest along the Maine Coast, with its deep carpet of moss, is much less inflammable than the same forest would be after some of the trees had been cut and the light which is thus let in had partly dried out the forest floor.

The earliest record was, fortunately, made by Champlain (1613) in his account of the voyage on which he discovered the island. He writes under date of September 5, 1604:

> "The same day we passed near to an island some four or five leagues long, in the neighborhood of which we just escaped being lost on a rock that was just awash and which made a hole in the bottom of our boat. From this island to the mainland on the north the distance is not more than a hundred paces. The island is high and notched in places so that from the sea it gives the appearance of a range of seven or eight mountains. The summits are all bare and rocky. The slopes are covered with pines, firs, and birches. I named it Isle des Monts Desert."

It thus appears that the island was covered almost completely with forest, except for the bare granite summits. From what we know of the virgin forest of the region we can picture to ourselves what Champlain probably saw. The "firs" which he speaks of must have been balsam fir and spruce, both red and white, which probably formed a more or less uniform canopy

above which towered here and there giant white pines. The birches indicate past fires, since in very old forests they are crowded out, or reduced to inconspicuous scattered individuals, by the conifers.

The bare rock of the summits, though conspicuous, was less in evidence than it is today. The white man has extended the area of the barren places by fire and cutting.

Fortunately, we possess a second account of the island written by a French friar only nine years after Champlain's visit. The expedition under de la Saussaye, sent out by Mme. de Guercheville, was caught in a fog on its way from the new settlement at Port Royal (in what is now Nova Scotia) to its intended destination up the Penobscot River to the present site of Bangor. When the fog lifted they found themselves off Mt. Desert Island at a point which is supposed to be the present site of Bar Harbor, or Hull's Cove, and which they called St. Sauveur, a name which they later transferred to their short-lived settlement at the mouth of Somes Sound. Father Biard (Sawtelle, 1921) thus describes what he saw:

"There in all the glory that spring imparts to hillside and valley lay the island of the Desert Mountains, *its tall pines and pointed firs, mingling with birches, whose lighter shades made marked contrast with the darker evergreen;* while *barren summits*, catching the rays of the hidden sun, gleamed like hammered brass." The italics are ours.

The picture agrees with that described by Champlain. There were also other types of forest which, since they were not on the slopes, were not visible from the sea. In the valleys and lower slopes on both sides of Pemetic there must have been bodies of beech, yellow birch and sugar maple with an admixture of red spruce, and probably also an occasional giant white pine. A remnant of this forest, without the pine, may be seen today just south of Eagle Lake along the carry trail to Jordan Pond. In certain of the swamps there were stands of nearly pure white cedar or arbor vitae, some of the trees of large size. Probably cedar also grew scattered throughout the rest of the forest as it does today. There must also have been groups of pitch pine, though probably less than now, and scattered red or Norway pine. There may also have been stands with considerable quantities of red oak, if the names such as Oak Hill, and some of the present forests, are reliable indications.

From 1613, when the English under Captain Argall destroyed the precarious French foothold at Somes Sound, the island appears to have been practically uninhabited by white men for about a hundred and fifty years. In 1689 the island was granted to Sieur de la Mothe Cadillac by Louis XIV

and from the Andros census (Hutchinson Papers) we are led to assume that Cadillac and his wife were living on the island in 1688, though his stay must have been brief since he was in France in 1689. In his account of the island, Cadillac says "Good masts may be got here and the English formerly used to come here for them." Therefore, although the island was not inhabited by white men, it was occasionally visited, and some of its trees were cut. These were probably only a comparatively small number of selected spruces and white pines, the removal of which had practically no effect on the forest.

The annals of the first permanent settlers begin after 1762, which may be taken as the starting point for the white man's influence on the vegetation. Probably white men started living on the island some years before this, but we have no records showing when or how many there were. The early settlers appear to have depended to a large extent on the wild grass of the marshes for hay to feed their stock. This wild hay seems to have been useful not only to the dwellers on the island itself but to those of the adjacent mainland, if we may judge by a petition sent by the islanders to Governor Bernard in 1768 complaining against these raids or "In Crossins" of the mainland settlers which threatened the stock on the island with starvation.

The value of the forests was recognized from the beginning. The same petition seeks protection from mainland trespassers who cut timber as well as from those seeking hay. It is stated that this cutting of the timber, which includes "staves, shingles, clapboards and other lumber," will "discourage future settlers." It is evident that the earliest comers depended largely on the plant resources which nature had grown on the island through the long period of years when it was unoccupied, and then used only by the Indians for hunting.

The wild hay gave food for the stock, and thus indirectly to its owners. But no doubt the main reliance was the crops raised on the more level and promising bits of land which had to be cleared. The proportion of level land on the island is not great, and that which is fertile is smaller still. Thus the food which can be produced will support only a comparatively small population. The fisheries comprised an important means of livelihood, and largely supported the small villages along the shore. But the main wealth of the island lay in its forests, as it still does, if we except that brought in by summer visitors.

It is not difficult to picture to ourselves the kind of cuttings which took place from the early settlements to the present time. There were none of the usual large operations by which extensive areas are stripped to feed a big mill which cuts and ships vast quantities of lumber and is then abandoned

when the surrounding territory is "cut out." Fortunately, the coast of Maine, as well as the rest of the state, largely escaped the "boom" type of development which makes flourishing lumbering towns for a decade or two and passes on leaving a virtual desert behind, as in Pennsylvania, the Lake States and now the Southern pineries.

On Mt. Desert Island the lumbering was never, happily for the island, on a scale comparable with that in Pennsylvania, or even in other parts of Maine. At first it was probably largely for local consumption, and the logs were cut at small mills run by water power. Later, the operations seem to have increased in size, and much or most of the lumber was doubtless shipped out of the island. By 1870 there were two steam sawmills, one at Salisbury Cove and the other at Pretty Marsh, and ten water sawmills (Street, 1905, p. 309). This may not represent the maximum of the island's lumber production, which perhaps came some time earlier. Whatever the amounts cut from year to year, it is certain that the island has been steadily producing more or less lumber from the time it was first settled to the present day. Although there has been no attempt to exercise forethought, the size of the cuttings has been small enough not to take all the mature growth before the second growth was ready to use. The greatest destruction has been from fire, which has swept over a large part of the island thus materially reducing the available stock of growing timber. The effect of these fires on the vegetation will be dealt with more fully in another place.

In the earlier cuttings, in fact until rather recently, the forests were not cut clean because the demand for the products was limited. At first they were skimmed of the very large white pine which commanded a ready and profitable market both in this country and over seas. These trees were found as scattered individuals throughout the forest, or in small groups. There may also have been here and there nearly pure stands of white pine, or at least stands in which a large proportion of the volume was white pine. A remnant of such a stand has been fortunately preserved around Fawn Pond. Here the bulk of the forest is made up of very large old white pine trees such as must have been common over the island when Champlain sailed past. The removal of the scattered pines made only rather small holes in the forest canopy, which soon closed up leaving a uniform cover of spruce and fir. Under this cover there could be little reproduction of white pine because of the shade. It could seed in only where the cuttings made openings large enough to let in the sunlight, or where several large spruces happened to be blown down by the wind or died from other causes.

The cutting of these large trees must have begun soon after the island was settled. The more accessible ones were of course taken first. Just how long

it continued we do not know, but probably before the middle of the nineteenth century only those large pines on the steeper and more difficult slopes were left. The remnants we have today happen to be on property from which the owners for some reason or other did not sell the timber.

The next phase consisted of going through the same forests in order to take out the larger and finer spruces for sawing into lumber of various kinds. Some of the larger spruce trees were doubtless cut under the earlier operations on which the main objective was the pine, but spruce lumbering does not appear to have been general until the large pine was about exhausted. We do not know just when the second phase began, but probably around the middle of the nineteenth century.

The effect of the removal of these larger spruce trees was to open the crown canopy considerably more than when the old pines were cut. This gave an opportunity for spruce and fir seedlings to spring up in the openings, and, in the larger ones, no doubt a certain amount of pine seeded in. In the moister places young hemlock became established. The danger of fires was materially increased by the dead tops lying on the ground and the drier conditions in the openings. Although the conditions favoring fire were not so bad as those following the heavier cuttings of later days, yet some of the severest fires known on the island came during this period. In 1848 a fire, started by a small boy, swept over the mountains of the northeastern part of the island. In 1864 a conflagration utterly destroyed the lumber business of the Jordan brothers on Jordan Pond, and burned the slopes of Penobscot (Jordan) and Pemetic Mountains, as well as much neighboring forest. These and other fires seem to have killed most of the remaining virgin white pine. In places the accumulated humus on which the trees were growing was burned out, leaving only the bare rock. The slow process by which this bare rock is re-clothed will be described in another section.

As the prices for lumber advanced, and the amount of large timber diminished, more and more of the smaller spruces were cut, and even the fir. The transition appears to have been gradual, and by about the nineties the smaller as well as the larger spruces were being taken, though the forest was by no means cut clean. Thus the third phase grew gradually out of the second.

The third phase corresponds with an increased fire danger, since a great deal more slash was left, and the more open condition of the forest permitted more rapid drying. There appear to have been many bad fires at the time this type of operation was carried on, perhaps the worst of which was the Cadillac (Green) Mountain fire about 1889, though whether or not this was directly attributable to logging we do not know.

Those areas which had the good fortune to escape fire became restocked with spruce, fir and white pine, and, in the moister places, hemlock. Owing to the greater amount of light, the proportion of deciduous trees was greater than after previous cuttings. The new forests contained, mixed with the conifers, a considerable proportion of red oak, red maple, white birch, and, in the more sheltered spots, yellow birch. Beech and sugar maple were abundant in the moister protected spots; not that their restocking was favored by the larger openings since they are shade-enduring trees, but they were given more opportunity to develop.

The fourth phase grew up recently with the development of the market for pulpwood, which takes the small spruce and fir, and with the demand for lower grade lumber. The spruce and fir are cut, sometimes peeled, sometimes not. and hauled out to the road. For lumber, small portable sawmills move from place to place wherever a tract of sufficient size to justify setting up can be found. Everything down to even three inches at the small end is sawed up. This is because of the practice of sawing " in the round " or " sawing alive," that is, without previously taking off a slab to square up the log. Obviously this results in utilizing much material which under the older methods was left in the tops to rot in the woods. Furthermore, it increases the amount which can be cut out of the logs by saving much of the part that formerly was thrown away as slabs. The deciduous trees, birches, maples, etc., are cut up into cordwood or sometimes left standing.

This modern method of logging makes a practically clean cutting, nothing being left except the defective and very crooked trees, and sometimes the hardwoods. It results in considerable quantities of slash, which in the township of Bar Harbor must be disposed of, generally by piling and burning, but in the two other towns can be left as a fire trap. Although the result, even when the slash is eliminated, is unsightly and appears like ruthless devastation, the forest does not suffer as much as would appear—provided fire is kept out. There generally follows an abundant restocking of white pine, spruce, and fir, with red pine on the drier sites, and hemlock on the moister. Fortunately, the sentiment in favor of fire protection has become so much stronger, and the methods of protection so much more efficient, that the danger of fire, though by no means negligible, is comparatively small. For the improvement with regard to fires a great deal is to be attributed to the influence of the Lafayette National Park rangers, who, in the course of their regular duties, are able to detect fires anywhere on the island as well as in the Park itself. The example of the Park officials in extinguishing fires is followed by private owners.

The cutting and burning of the forests, briefly outlined above, has been to

a certain extent responsible for the kinds of trees which grow on various parts of the island today. The natural course of development which had been going on from the time the land was bare after the retreat of the ice, until it supported the highest type of forest of which the climate is capable, was arrested and thrown back. This will be considered more fully below. Suffice it here to say that the stretches of birch and aspen forests which cover such a large proportion of the island with growth of little value are to be attributed to past fires. The cuttings alone, without the fires, would have given young forests of the more valuable species instead of the nearly worthless birch and aspen, much of it gray birch which is hardly fit even for firewood.

Pitch pine, a picturesque tree, but of no value here since it seldom reaches sufficient size to be worth sawing into even low grade lumber, has most probably increased in area since the arrival of the white man. This is because the barren rocky places on which it will grow, but where other trees are unable to survive, have been considerably increased by human interference, chiefly by fires. The tree was no doubt fairly abundant before the white man came, since the barren summits which Champlain mentions indicate the presence of sites suitable for it, but it has been given a greater opportunity to spread than it had before.

With the spread of pitch pine there has been an extension of the plants over and among which it grows—its associates. Many of these are coastal plain species common in the sand plains of New Jersey and Long Island. Among these might be mentioned the huckleberry, *Gaylussacia baccata,* very abundant under the pitch pine and elsewhere on the island, the bearberry, *Arctostaphylos Uva-ursi,* which extends even to California under moderately dry pine forests, the yellow flowered heather-like *Hudsonia ericoides,* and others. Man's interference has thus caused an increase in many coastal plain plants which thrive on the drier sites. The scrub oak, *Quercus ilicifolia,* seems to be an exception in that it is confined to a single mountain, Acadia (Robinson). But it may be that even this plant was more restricted in the past than it is today.

Man's influence on the vegetation has not been confined to the effects of cutting and burning the forests, though the greatest change resulted from these two agencies. On Mt. Desert Island, as on many other islands along the Maine Coast, there used to be a good deal of sheep raising. Sheep seem to have been introduced by the earliest settlers, and were not given up until recently, when it appears that certain restrictive laws made the industry unprofitable. Since these forests, unlike the more open forests of the west, are unsuited to grazing, the sheep must have been largely confined to lands cleared for pastures, and to old farms which had been abandoned. They may,

however, have had some effect in furthering the spread of certain plants, particularly those which do best in the more open places.

Clearing of land for cultivation must be considered an important factor in changing the vegetation, but the extent of its effect depends upon the extent of the land suitable for farming. In some parts of the country, as in the middle west and the eastern edge of the plains, where most of the land is valuable for crops, the native vegetation has been almost totally destroyed. Scientists endeavoring to find what the soil and climate will produce under natural conditions are constrained to study strips along the railroads as the nearest approach to remnants of the native plants. On Mt. Desert Island the area which was cleared and devoted to crops and pastures was larger in the past, before the opening of the west, than it is today. As with the rest of New England, a considerable proportion of the farm-lands has been abandoned and allowed to revert to forest. Prof. R. T. Fisher, director of the Harvard Forest, has stated that the 200,000,000 board feet of white pine which is yearly cut for box boards in Massachusetts comes practically all from land which was in farms at the time of the Civil War. The amount of coniferous forest on Mt. Desert Island abandoned farms, while much smaller in proportion to the total area than on similar land in Massachusetts, is considerable. In many cases the re-establishment of the forest has gone so far that it is practically impossible to tell from present appearances whether or not the land was once cleared. Since the forest on such lands does not appear to differ markedly from that on other parts of the island, no attempt has been made to map or study it separately.

GENERAL CHARACTER OF THE PRESENT VEGETATION

The present vegetation, with its variety of conditions and aspects, should not, of course, be considered by any means permanent or static—as it so often seems. We recognize that we are dealing with an ever-changing living thing, a flow rather than a set of fixed points, except for the climax types which will probably remain essentially unchanged for a very long time (Cooper, 1926). Aside from the climax, the present vegetation at any one spot is but a single stage of the steadily continuing succession. When we look at the present stage it is just as if we took out one single picture from the thousands that pass in a motion picture film. The progressive development, or succession of the vegetation, from the simpler forms with modest requirements which start on the bare rock or soil, to the highest or climax for this particular region, will be described more fully below. Here, for the sake of clearness and simplicity, we will imagine that the course of succession has been arrested for the moment, and consider the different types of vegetation as we find them.

DISTRIBUTIONAL RELATIONS

Let us first consider where the Mt. Desert Island vegetation fits into the general scheme of the vegetation of eastern North America. There have been a number of attempts to divide the country into regions, each scheme differing in certain respects from the other in accordance with the viewpoint of the individual investigator. Though the subject is intensely interesting, and of fundamental importance, we will not take up time and space with discussions which can be found elsewhere (Hawley and Hawes, 1912, Hill, 1923, Nichols, 1918, Shreve, 1917, Transeau, 1905, Zon and Sparhawk, 1923). Our investigation has not led us to draw up a new classification, no doubt fortunately, though we differ a little from students of nearby localities in our conception of the ultimate climax toward which the vegetation is trending, as will be discussed below on pages 83, 86, and 124.

The two main viewpoints are those of, first, the plant geographer (the plant ecologist) who studies the distribution of plants and the causes underlying distribution, and, secondly, the forester, who is primarily interested in the practical application of the facts of distribution. The former sees the vegetation in relation to the past and present forces which are acting upon it, the latter is often obliged to confine his attention to a comparatively small number of the commercially important trees.

The forests of eastern North America have been divided by Nichols (1918 pp. 257–261) into two broad climatic regions with a transition zone between. He recognizes an Evergreen Coniferous Forest in the north extending from the tundra to the St. Lawrence and Laurentian Plateau, and a Deciduous Forest Region in the south extending from southern Florida to a line which corresponds with the southern limit of balsam fir, passing through southern New England, making an arm south along the Appalachian Mountains, then westward from about central New York State. In between these two widely separated lines, formed by the northern limit of sugar maple and southern limit of balsam fir, is the large territory assigned to the Transition Forest Region, which includes Mt. Desert Island. Here the conifers extend southward, and the deciduous trees northward. The predominant conifers in the northern part of this Transition Region are spruce and fir, in the southern part white pine; the deciduous species in the southern part are many, principally the oaks, tulip, hickories, ashes, and so forth; in the northern part they are beech, yellow birch, and sugar maple. In this Transition Region the deciduous trees advancing north, after being driven south by the glaciers, have telescoped with the coniferous trees which followed the retreat of the ice. The combinations of plants are different in various parts of the Transition region, both because of the range of climate they cover, and also on account of the varying soil and topographic features. Nichols' division is based upon the distribution of certain trees rather than on temperature, moisture or some other physical factor, and is broader than the divisions based on rainfall and evaporation by Transeau, Shreve and others. Its advantages are its simplicity and recognition of the fact that development (succession) may be arrested indefinitely on poor soils or unfavorable sites.

Shreve (1917, see map) places most of the state of Maine, including Mt. Desert Island, in the Northeastern Deciduous-Coniferous Transition Region, on the basis of rainfall-evaporation ratios. Though his viewpoint differs from that of Nichols, and he gives more detail, the result is essentially the same.

Zon and Sparhawk (1923, p. 522), taking the forester's viewpoint, place Mt. Desert Island at the southern extension along the Maine coast of the Spruce-Fir-Northern Hardwood (Northeastern Hardwood and Coniferous Forest) Region. By Northern Hardwoods is meant beech, yellow birch and sugar maple, as distinguished from the more southerly hardwoods such as various oaks, hickories, tulip, ash and so forth. Their map corresponds with the broader features of the forest as we actually find it on the ground more closely than Shreve's. That of Nichols did not even attempt a subdivision into broad forest classes.

Hawley and Hawes (1912, see map), from the forester's viewpoint of the present commercially important trees of New England, place Mt. Desert Island in the Spruce Region. This practically coincides with Zon and Sparhawk's Spruce-Fir-Northern Hardwoods. The name Spruce Region is justified by the fact that this is the principal tree which the area produces, because the hardwoods under present conditions can not be taken out. Coniferous logs are floated down the streams to the mills or railroads, and the hardwoods will not float.

Mt. Desert Island may then be considered as belonging either in Nichols' large Transition Forest Region, in Shreve's Transition Region, in Zon and Sparhawk's Spruce-Fir-Northern Hardwoods, or in Hawley and Hawes' Spruce Region. Perhaps Nichols' classification best fits the developmental viewpoint, when his large region is subdivided to correspond with the various differences which occur and which it seems unwise to ignore. Thus the northern extension of his Deciduous Forest Region into New Jersey, where it includes pitch pine, is really a northward extension of the coastal plain pine belt. Quite possibly this belt is due to soil conditions which prevent the forest reaching the deciduous climax stage, but it should be recognized as at least an important subdivision of the Deciduous Region. The southern part of the Transition Region should be subdivided from the northern part on account of the differences in species already noted. The portion containing oaks, hickories and tulip could be separated from that in which these trees are lacking, but which contains red spruce. Possibly the occurrence of red spruce is sufficient to distinguish the northern from the southern portion. A white pine subdivision, reaching from northern Connecticut to Penobscot Bay and including parts of Vermont and New Hampshire, might possibly be recognized. This is largely a case of arrested development similar to the hard pine forests of the coastal plain, though much smaller and not continuous, since it occurs on separate stretches of sandy soil. The northern hardwoods, where spruce forms only a small percentage of the stand or is lacking, is an important subdivision, from an economic standpoint, extending from northern New York to central Maine. Nichols' Transition Forest Region would thus be subdivided into four parts: Southern Hardwoods, Spruce and Hardwoods, White Pine, and Northern Hardwoods.* Our island would be in the Spruce and Hardwoods subdivision.

* The Spruce and Hardwoods, and Northern Hardwoods, are not wholly distinct geographically, but intermingle to a certain extent. Since the occurrence of the Spruce and Hardwoods does not always seem to be due to altitude or climatic causes, and may be due partly to soil, it would be possible to combine these two subdivisions into a Spruce and Northern Hardwoods subdivision.

·Forest Types

Mt. Desert Island enjoys the distinction of bearing types of vegetation which are found in all three of Nichols' large regions, and in three out of the four subdivisions. The Deciduous Region is represented, curiously enough, by a conifer, pitch pine, which characterizes the more sterile portions of the coastal plain soils of this region in New Jersey. The three subdivisions of the Transition Region represented are: the White Pine, the Northern Hardwoods (to a limited extent and probably due largely to the removal of the spruce) and Spruce and Hardwoods, the last by the Northern Hardwoods-Spruce type. Examples of the Nichols' Evergreen Coniferous Forest Region may be seen along the shores in the stands of white spruce and fir, and the mats of crowberry along the rocks, as well as in the black spruce which grows in certain of the bogs.

The dominant tree over the island is red spruce, as it should be from the location of the island in the northern subdivision of the Transition Forest Region. The bulk of the forest, aside from burns, is made up of a mixture of varying proportions of red spruce, white pine, red pine, white cedar, white spruce, and occasionally hemlock, with a good deal of red maple, white birch, gray birch, red oak, and some aspen. These deciduous trees show up strongly in numbers, but seem to be more or less temporary, and to have come in largely as a result of human interference.

This mixture, since it does not fit with any of the types recognized by foresters, has been for the sake of clearness considered by itself as the Mixed Conifer type. But it crystallizes out, on different sites, into five easily recognized and distinct types representing different conditions of the habitat. These conditions and their relation to the different types constitute one of the principal parts of this study, and are treated more fully below. For the present it will suffice to give briefly the more salient general characteristics of each type. The classification used is that formulated by the Committee on Research of the New England Section of the Society of American Foresters (Hawley, Terry and Woodward, 1922), with certain modifications in the percentages of species in some of the types to fit local conditions. Since the general make-up of the types fits the Committee's classification, the small change in percentages seems justified on the ground of simplicity and to permit comparison with the same types of forest in other parts of New England. Burns have been classed separately since it is not always possible to determine the type in which they belong. The percentages refer to the number of individual trees of the different species rather than to their vol-

ume.* Only the trees forming part of the main forest canopy, that is, the dominant or subdominant trees, not the understory, suppressed trees or reproduction, are counted. The colored map at the beginning of this *Memoir* shows the proportionate area occupied by each type.

Spruce. The spruce type is made up of 70 per cent† or more of red spruce or white spruce, or both. The trees in mixture are balsam fir, white pine, white cedar, hemlock, paper birch, aspen (both *Populus grandidentata* and *P. tremuloides*), red maple, occasionally red oak, gray birch and rarely red pine. In general, this type corresponds with the "spruce slope" of other parts of Maine, rather than with the spruce flat, though the latter is represented in small amounts.

Some of the stands are on old cuttings and others on abandoned clearings. It was not considered necessary to separate out the latter as the Committee on Research has done. There are some virgin stands left, the largest being on Western Mountain, fortunately included within the National Park.

Fir. On the level summit of Cadillac (Green) Mountain is a small remnant of the fir type. Though insignificant in proportion to the other types on the island, this bit of forest is of interest for its resemblance to the upper slopes of the northern New England and New York mountains, where the red spruce is giving way to the balsam fir, which a little higher forms pure stands (Adams and others 1920). The composition of this survivor of the fires which have swept over Cadillac Mountain is: balsam fir 66 per cent, red spruce 29 per cent, white birch 5 per cent.

Northern Hardwoods-Spruce. Yellow birch, beech, sugar maple and red spruce in varying proportions. A characteristic feature of this type is the abundance of sugar maple reproduction. A ground cover of American yew or ground hemlock, *Taxus canadensis,* is also characteristic, but is not confined to this type. A considerable amount of scattering hemlock, and an occasional white ash, *Fraxinus americana*, are also found. The type is restricted to a small patch of about 20 acres in the carry between Eagle Lake and Jordan Pond (marked Hadlock Valley on the trail map) and a small spot

* There is sometimes a great deal of difference between the results obtained by these two methods. For example: a stand may be made up of small spruce trees among which is a scattering of very large white pines. On the basis of numbers of individuals such a stand might show 90 per cent spruce and 10 per cent white pine; while on the basis of volume the same stand would show only 40 per cent spruce as against 60 per cent pine. Such cases are not uncommon on Mt. Desert Island. Obviously, the method used depends on the purpose of the classification. For commercial use it is more important to know the volume than the number of each species.

† The Committee gives 90 per cent for spruce slope and spruce flat.

in the notch between Norumbega (Brown) and Parkman (Little Brown) Mountains. Those parts now marked as Hardwoods in the valley south of Bubble Pond, and also along the east shore of Eagle Lake probably belonged to this type before being cut over.

Hardwoods. Beech and yellow birch with a little sugar maple. That part of the type which has this composition represents the Northern Hardwoods-Spruce from which the spruce has been removed. There is also a different forest which has been included with the hardwoods to avoid too many types. This is predominantly red oak, with beech, a little yellow birch, and spruce in mixture. It also contains considerable amounts of red maple and white birch, with a scattering of white pine, and in places a little sugar maple. It is a cut over forest probably intermediate between northern hardwoods-spruce and mixed conifer.

White Pine. Stands containing 70 per cent * or more of white pine. The principal coniferous associate is spruce, though red pine is sometimes abundant, especially on the drier sites or where the stand has been heavily opened in the past. White cedar is common; fir is scarce in the canopy, but predominates in the reproduction under the shade. The deciduous associates are red maple, gray birch, red oak and white birch.

The amount of this type is comparatively small. If volume, rather than number of trees, were considered, it would be at least doubled, taking in areas now mapped as mixed conifer. If the deciduous trees, most of them small and worthless, were left out, additional areas would come into the type. Some of the type is on land which may formerly have been cleared.

White Cedar Swamp. White cedar, *Thuja occidentalis,* forms 80 per cent or more of the stand. The trees in mixture are red spruce, white pine, fir, red maple, white birch, sometimes aspen and ash.

Although white cedar is common practically all over the island, it forms pure, or essentially pure, stands only in the swamps. These swamps appear to be well drained, and, although the surface sphagnum, where it occurs, is strongly acid, the substratum seems to be generally neutral. In other words, the cedar here will tolerate high acidities, but prefers neutral soils.

Mixed Conifer. Varying proportions of conifers, totaling 50 per cent or more. The principal conifers are red spruce and white pine, with mixtures of cedar, red pine, fir and occasionally hemlock. The most abundant hardwoods are red maple, and red oak, with a good deal of white birch and gray birch, some aspen and a little beech.

The proportions of the different conifers vary with the site, white pine being more abundant on the drier places, and spruce on the moister. Cedar

* The Committee gives 80 to 100 per cent.

comes in to a certain extent even on the apparently drier sites; hemlock is confined to localities where moisture is abundant.

A glance at the map will serve to show that this is the most abundant type on the island, aside from burns, a considerable proportion of which will eventually bear mixed conifer stands.

Pitch Pine. Stands containing 80 per cent or more of pitch pine. Pure stands are more common in this type than in any other except spruce—the opposite climatic extreme. The associates are scattering red pine, white pine and red oak, with an occasional spruce and fir, and sometimes red maple.

The type is confined to the rockier and more barren places, on south exposures or level spaces. It is not found on rocky north exposures, which generally grow up to mixed conifer. Sometimes, as along the Ocean Drive north of Thunder Hole, it comes close to the sea where one would suppose there was insufficient warmth.

Burns. The burns may be divided into two broad classes on the basis of moisture, though the separation is not shown on the map.

On the drier sites gray birch predominates, forming 70 per cent or more of the stand.

On the more favorable sites, possibly cooler as well as moister, white birch and aspen together comprise 30 per cent or more of the canopy.

The conifers are coming back under the burns wherever there are seed trees in the vicinity and other conditions are favorable, but, unfortunately, some very large stretches occur under which there are none of the more valuable species.

Three non-forested classes have been recognized and mapped. These are of considerable importance in unravelling the developmental relations of the vegetation, as will be seen later on. They are as follows:

Bog. Chiefly sphagnum, with various shrubs, mostly ericaceous, over a substratum of peat of varying depth and of high acidity. They contain a scattering of stunted spruces, black or red, larch, and white pine.

Marsh. The marshes are distinguished from the bogs by their better drainage and the preponderance of sedges instead of sphagnum and ericaceous plants. They are alkaline where sea water penetrates.

Rock. Ledge, cliff or talus slopes. The appearance is barren, but generally lichens are found growing on the rock surfaces, and frequently herbs, shrubs and even trees find a foothold in the crevices.

THE ENVIRONMENT

General Climate of Mt. Desert Island

Our knowledge of the general features of the climate of Mt. Desert Island is limited to a set of records secured by Mr. George B. Dorr and his father in cooperation with the Weather Bureau for the period from 1886 to 1908 inclusive, or 23 years. It is to be regretted that the parsimony of Congress prevented their allotting the Weather Bureau sufficient funds to continue these observations. It is earnestly hoped that some day the Weather Bureau may be granted a sufficient appropriation to continue this extremely important work, rendered all the more necessary by the scientific interest of the Lafayette National Park.* Fortunately, the observations which have been taken give fairly trustworthy information on precipitation and temperature, the two most important climatic factors so far as we are concerned.

Although an island in the sea, the climate of Mt. Desert, in common with that of our Atlantic Coast, is to a considerable extent continental, particularly in winter. This is because our storms and our fair weather—cyclones, or low barometric pressure, and anticyclones, or high pressure—come from the west and pass over New England on their way out to sea. The storms draw in air from the sea and give ocean winds, but the anticyclones bring northwest blasts from the cold interior of the continent. This, as mentioned briefly above in speaking of the former coastal plain, accounts for the coldness of the waters of the Gulf of Maine rather than the arctic current, as had been supposed. But in summer, when the sun rather than the cyclones and anticyclones controls the weather, the climate of the island is largely dominated by the sea. The prevailing winds are southwest, and must pass over the cool waters of the Gulf before reaching the island. Thus the shore is the coldest part of the island in summer, the winds being warmed as they pass over the sun-heated land. This point has an important bearing on the distribution of the types of forest, and will be discussed more fully below in the interpretation of the detailed climatic records.

The surface temperature of the Gulf waters at Mt. Desert Rock, 25 miles south of Mt. Desert Island, is comparatively uniform and low throughout the year. We are fortunate in having records taken at the lighthouse during 1881 to 1885 inclusive, except during the months of January and February. These records show a range of only about 18 degrees Fahrenheit between the

* Daily precipitation, and temperature, cloudiness and wind are now being recorded.

fifth of March and middle of August, from approximately 35° to 53°. Since a maximum of 53° for the surface of the water in mid-summer is distinctly cold, we can readily understand the cool summers which prevail along the Maine Coast. The air temperature at Mt. Desert Rock fluctuates much more than that of the water, as might be expected. However, it reaches a maximum of only 68° F. in the middle of July, taking the average for 1881–83. At Matinicus Rock lighthouse, southwest of Mt. Desert Island, the temperature of the surface water from 1881–85 was essentially the same as at Mt. Desert Rock, but the highest air temperature for 1881–83 averaged only 62°.

PRECIPITATION

The average annual precipitation on Mt. Desert Island from 1886 to 1908 was 48.3 inches, enough for a rather rich vegetation characteristic of moist conditions (mesophytic). The lowest during this period was 42.33 inches, not very much below the average, and the highest 60.04 inches. The distribution throughout the year is not as favorable as it might be, the two months showing the lowest amounts, June and July, being the ones when the rain is most needed. The distribution is somewhat erratic; during the year with the highest precipitation (1900, 60.04 inches) the months of July and August were very much drier than the average for the 23 years, and September was a little drier, the high figures being piled up during January, February, March and October. Likewise in the driest year, 1886, certain months were wetter than the mean. (See Table I.) The following table gives the mean precipitation by months from 1886 to 1908, the driest and wettest years, and the average number of days in each month with .01 inch or more of precipitation.

TABLE I. *Mean monthly and annual amounts of precipitation, in inches, for Bar Harbor, Maine, 1886 to 1908 inclusive. Also the driest and wettest years and average number of days with .01 inch or more*

	Jan.	Feb.	Mch	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec	Annual
Mean.....	5.35	4.40	5.46	3.06	3.54	2.93	2.87	3.14	3.59	4.29	4.85	4.82	48.30
Driest year, 1886	9.29	5.89	3.28	1.07	3.90	1.75	1.51	1.44	2.58	2.58	5.74	3.30	42.33
Wettest year 1900.........	11.15	6.20	8.57	3.15	6.07	3.52	1.65	1.90	3.15	6.77	5.48	2.43	60.04

Average number of days with .01 inch or more of precipitation

	10	10	11	8	9	9	8	7	7	9	9	10	107

The precipitation at Bar Harbor is higher than at the two other stations along the Maine Coast, Portland 42.63 inches, and Eastport 42.90. Yet Bar Harbor enjoys considerably more fair weather, with only 107 days in the year having .01 inch or more precipitation, as against 135 days for Portland and 152 days for Eastport. Evidently it rains or snows less often but harder at Bar Harbor than at the two other points.

The amount of the precipitation which comes during the growing season is considered by some as being just as important, or more so, than the total amount for the year. But it must be remembered that in climates where the winter precipitation comes as snow, the water is stored on the surface of the ground until the reviving warmth of spring melts the snow and allows it to soak into the ground to furnish water for growth. Of course, a large proportion, which varies in different years according to the rate of thawing, runs off into the streams as spring freshets, and is lost. Just what percentage of the total snowfall becomes available it is impossible to say, but it is large enough to be of considerable value.

If we take the growing season (see below) as the five months from May to September inclusive, we find that this season receives only 16.07 inches of precipitation as against 32.23 inches for the dormant season. Thus, although the growing season is five months long, or nearly half the year, it receives only one-third of the annual precipitation. The melting snow might bring this proportion up to half or about 24 inches, possibly even higher. This is not a very favorable distribution and accounts for the dryness of the woods in mid-summer and the consequent danger of forest fires.

TEMPERATURE

The temperature of Mt. Desert Island during the winter is influenced, though not altogether controlled, by that of the ice-bound mainland; during the summer it is largely determined by the cold waters of the Gulf of Maine. In general, the winters are not quite as cold as on the mainland, but the sum-

TABLE II. *Mean Temperatures for Bar Harbor, Maine, and Medford, Long Island. N. Y. Degrees Fahrenheit*

	Length of record, years.	Jan.	Feb.	Mch.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Bar Harbor .	20	21.0	22.0	31.4	41.5	51.6	59.3	65.5	64.3	58.9	47.8	38.1	26.2	44.0
Medford, Long Island.	15	30.0	28.7	36.9	46.4	57.7	65.7	71.9	70.4	63.8	54.7	42.9	33.0	50.2

mers are distinctly cooler, so that the means for the year are not very different. The mean temperatures by months and years for Bar Harbor, based on a period of 20 years, are given in Table II. The records for a part of Long Island have been added for comparison.

GROWING SEASON

The average length of the growing season, considered as the period between the average date of the last killing frost in the spring and the first killing frost in the autumn, is 129 days, from May 18 to September 24. Actually it is a little longer since in some plants, especially the trees, the sap starts to ascend before the last killing frost of the spring, and certain activities continue after the first killing frost of the autumn.

According to the widely used method of Merriam (1894) the effective temperature for this frostless period (the accumulated degrees of heat calculated for all the days when the mean temperature is above 42°) is 2765° F. for Bar Harbor. On the Livingston-Shreve (1921) method of temperature summation, taking 39° instead of 42° as the base, the figure is 3220° F.

The effective temperature for Medford, Long Island, with which we have compared certain other Mt. Desert factors of the environment, because pitch pine occurs at both places, is 3968°, while the Livingston-Shreve temperature summation method shows for Long Island generally 4738° F.

The foregoing figures of precipitation, temperature and growing season may be taken as indicating the broader general characteristics of the climate of Mt. Desert Island.

Environmental Factors in Representative Forest Types

The marked differences in the forest types already briefly described are obviously not accidental. They may be due to local differences in climatic factors, such as moisture, temperature, evaporation or wind. They may be caused by differences in soil conditions; or they may be the result of different methods of treatment in the past. Each forest type may be permanent, or may be merely a stage in the development of the forest from lower and more open to higher and denser forms. If the local climatic factors, aside from the influence of the forest cover, are essentially the same for all the forest types, the differences must be due to soil or past treatment. Differences due to soil will to a certain limited extent tend to disappear gradually through the action of the forest itself. The accumulation of humus will increase the moisture-holding capacity of very light porous soils, and will improve the aeration of very heavy soils. Rocky sites will improve through the disintegra-

tion of the rock by weathering, and accumulation of humus; wet sites will improve by building up through the accumulation of plant remains. But there are certain soil differences, particularly those associated with fertility due to the available plant nutrients contained, or to the presence or absence of toxic substances, which are for all practical purposes permanent. Infertile soils permit the development of the forest only to a certain stage below the climatic climax, a stage which is recognized as the physiographic climax (Nichols, 1923). Differences due to past treatment tend to disappear where the climatic factors and soil conditions permit.

Our problem was to find, so far as possible, what, if any, are the differences between the habitats on which the different forest types of the island are growing. Such information would be of much value in supplementing the usual methods of determining, by observation and comparison of the vegetation itself, whether a type is permanent or merely a stage of development. If marked differences are found in the open spaces, uninfluenced by the forest, the differences in forest types may be due at least in part to the habitat. If, on the other hand, the habitats are essentially similar, the forest types must be merely stages in a successional series.

SELECTION OF STATIONS IN FOUR REPRESENTATIVE FOREST TYPES

In order to ascertain possible differences between the environments of the various types of forest on the island, representative examples were selected for detailed study. The aim was to include forests which elsewhere grow in widely separated regions, since it seemed that the habitat of these forests on the island might reflect some of the characteristics of the region in which the forest grows. The two extremes were the pitch pine type, representing the most southerly set of conditions, quite different from those which prevail over most of the island, and the spruce type, representing the northerly extreme. Our pitch pine station was less than three miles in an air line from our spruce station. Yet what a stretch of country lies between the regions which each typifies—from New Jersey to the St. Lawrence. Our intermediate stations were, one in the white pine type, representing central New England, and one in a red oak forest which was selected partly to find its relation to the other types and partly because of its markedly different features. No station was established in the mixed conifer type, since, although the largest on the island and therefore probably controlled by conditions which fairly represent those for the island as a whole, it is extremely variable, and would obviously give a set of values somewhere between those for the pitch pine and the spruce. Just where, in between these two extremes, the values

would fall, would depend on the particular spot selected. Although no instrumental records were secured in the mixed conifer forest, yet it was studied in some detail, and is fully described below.

The four pieces of forest selected for study with the modest instruments at our disposal are each one typical of the same kind of forest elsewhere on the island, except the oak which probably does not fully correspond with the other stands of hardwoods. It is reasonable to assume that the environment at each of these selected examples is essentially similar to that of the rest of the corresponding type on the island.

It was important to find, so far as possible, the actual conditions of the habitat itself, aside from the influence which the forest cover exerts. These conditions are theoretically those which the forest must encounter in becoming established. For this purpose there was established, at each of the four kinds of forest selected for study, an open station sufficiently exposed to be out of the influence of trees.* Since the island is almost solidly forested, aside from cultivated fields, rock ledges and brush following burns, it was a difficult matter to find suitable openings. For the pitch pine and white pine it was necessary to use open rock ledges, which admittedly influenced the records owing to the heating of the rock by the sun. At the spruce station an open headland exposed to the sea had to be used. Here the occasional stunted and flattened trees indicated that the cause of this opening was partly the lack of soil and partly exposure to the sea. At the oak station it was possible to use an artificial opening in a hay field, which represented the open conditions fairly well.

THE FORESTS

The contrasts between the different types of forest which here and there crystallize out from the prevalent mixture will be evident from the following description of each of the four forests in which instrumental stations were established.

Pitch Pine

The site selected for the special study of the pitch pine forest was on the south slope near the top of Huguenot Head (Pickett Mountain) at approximately 650 feet elevation. The slope is extremely steep, made up of a series of granite steps, or short cliffs and narrow benches. Much of the granite

* During 1923, it was necessary to place the open station for the spruce in an opening in the forest which was less fully exposed than that used in 1921 and 1922, but the records seem to bear the same relation to those of the other stations as in the two preceding years.

is exposed, with only a cover of lichens, or completely bare. Soil is found only in pockets on the benches, and the trees in many places grow in the crevices of the rocks which they have lightly covered with a thin layer of débris in which huckleberry, ground juniper and other shrubs and herbs find a foothold (see Fig. 3).

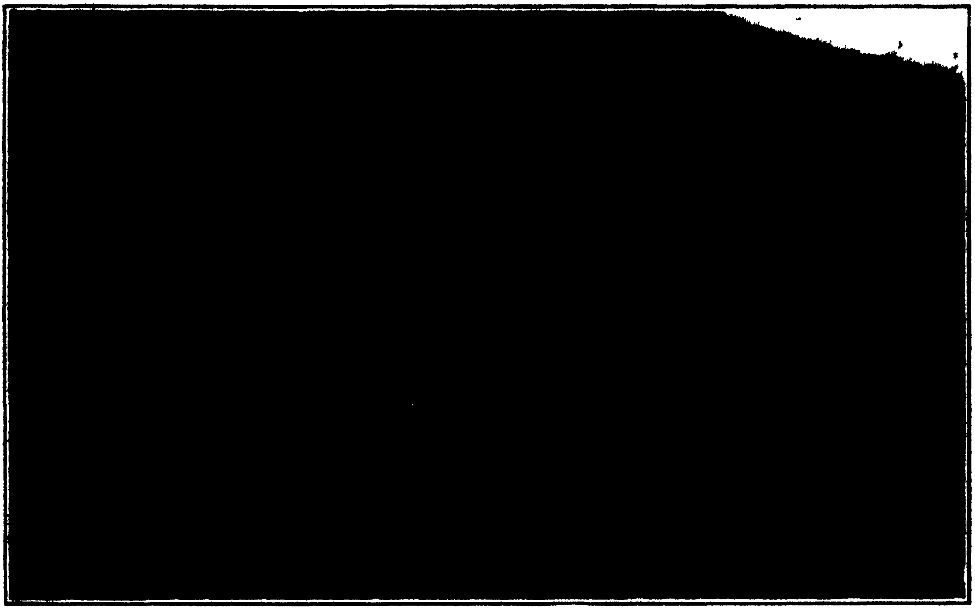

FIG. 3. Pitch pine open station on Huguenot Head (Pickett Mountain), showing rocky character of site. Livingston black and white atmometers in front of a ground juniper bush (*Juniperus communis depressa*). The top of a Bates evaporimeter is just visible to the left of the white atmometer. This picture shows also the early stages of development of vegetation. Lichens breaking down the rock to form humus and soil, and a later stage, colonization by woody vegetation in the locally favorable bench behind the instruments.

The stand selected for the forest station (Fig. 4) is just above the precipitous part of the hill, where the slope is less steep and there are occasional pockets of soil between the large flat ledges of granite. Except for the bare ledges, the slope is clothed with an open stand of stunted pitch pine. The trees run from 4 to 10 inches in diameter at 4½ feet from the ground, and from 12 to 22 feet in height. They are about 120 years old, showing rather slow growth.

The composition of the main stand, determined by a count of a sample acre around the station, is 98.6 per cent pitch pine, .7 per cent red pine and .7 per cent red oak. There are 165 trees per acre. The reproduction is

scanty, only 29 pitch pine seedlings per acre, probably on account of frequent fires in the past which do not kill the mature trees, but consume the young growth. A count of the reproduction is of interest in indicating the possible

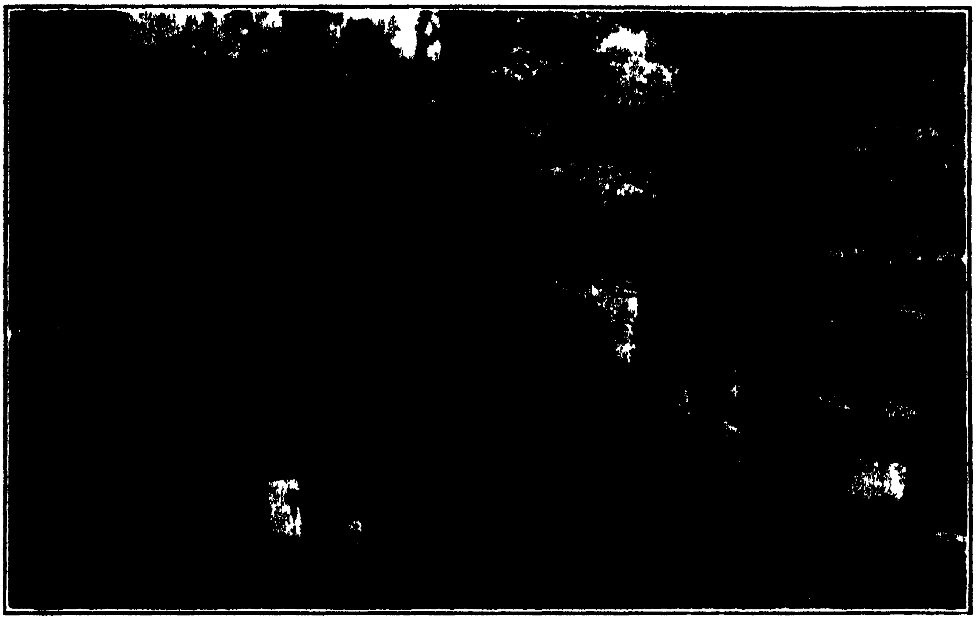

FIG. 4. Pitch pine forest station, showing open stand and short trees. Livingston atmometers in left foreground. Heavy undergrowth of huckleberry (*Gaylussacia baccata*) in background. Thermometers for soil temperature were under the huckleberry.

trend of development. It showed the following percentages: pitch pine 53, white pine 3.5, red pine 2, red spruce 2, gray birch 18, red oak 14.5, red maple 3.5, and bird cherry 3.5. It looks from these figures as if the stand were gradually going over to the mixed conifer type, but the white pine and spruce seedlings, now under the protection of the pitch pine, will have many vicissitudes to endure before they become mature trees.

The forest floor, where the instruments for measuring evaporation were placed, was covered with a thin layer of needles and grass. Elsewhere there was a dense growth of ground juniper, *Juniperus communis depressa,* and huckleberry, *Gaylussacia baccata,* with blueberry, *Vaccinium pennsylvanicum,* and bearberry, *Arctostaphylos Uva-ursi,* and other shrubs and herbs.

The spot selected for the open station, to represent the conditions which this forest must survive to become established, or the site factors uninfluenced by the trees themselves, was on a small bench about 200 feet from the forest station, farther down and on the precipitous part of the slope. It received

full sunlight all day, except that on the east Champlain (Newport) Mountain rose 35 degrees above the horizon, and on the west Flying Squadron (Dry) Mountain, farther away, rose 10 degrees. It was subjected to the full exposure of the wind through an arc of 155 degrees, from N. 70° E. around to S. 45° W. Thus it had the full force of the prevailing southwest winds which, coming off the sea, passed over 5 miles of land before striking the station. The slope below the station, on account of its considerable proportion of bare granite rock which became heated in the sun, exerted a considerable influence on the station. But many of the pitch pine trees on the slope were subjected to the same warm winds. On the bench where the instruments were set was a mat of ground juniper, with blueberry and bearberry (Fig. 3).

Curiously enough, this slope received a larger proportion of fogs than any of the three other forest types except the spruce. Since it faced the sea, the fogs were not intercepted, but rolled up against it while they were cut off from the white pine and red oak stations. It was by no means uncommon for the pitch pine station to be covered with dense fog while the white pine was in the open sunlight. Yet the pitch pine forest had every appearance of being drier than the white pine.

White Pine

The white pine forest selected for study (see Fig. 5) was on Bear Brook Hill at an elevation of 200 feet, about a mile south of the village of Bar Harbor and almost adjoining the Mt. Desert Nurseries, on land sloping gently to the southwest. The soil was a light, very porous, stony loam, which will be more fully described below.

The composition of the main stand showed the following percentages: White pine 74, red pine 9, red spruce 13, white cedar 4.

The white pines are from 7 to 20 inches in diameter at 4½ feet from the ground, and from 55 to 60 feet in height. The stand seems to be approximately even aged, and is from 60 to 70 years old.

The forest floor at the station proper is almost exclusively bare pine needles.

Some of the young firs which formerly grew under the shade of the forest have been cut. But a considerable number remains, enough to show that this tree made up a large proportion of the reproduction. Whether or not it would have survived and played a part in the second generation, is another matter. Probably few, if any, would have come through under natural conditions. In all the openings, even the small ones, white pine is seeding in

prolifically. Most of it is recent, 2 to 4 years old. The percentage composition of the reproduction should not be relied upon too strongly as an index of the future stand because of the high mortality. A sample where but little fir had been cut out is as follows: white pine 53, fir 34, red spruce 4, cedar 4, red oak 3, red maple 2.

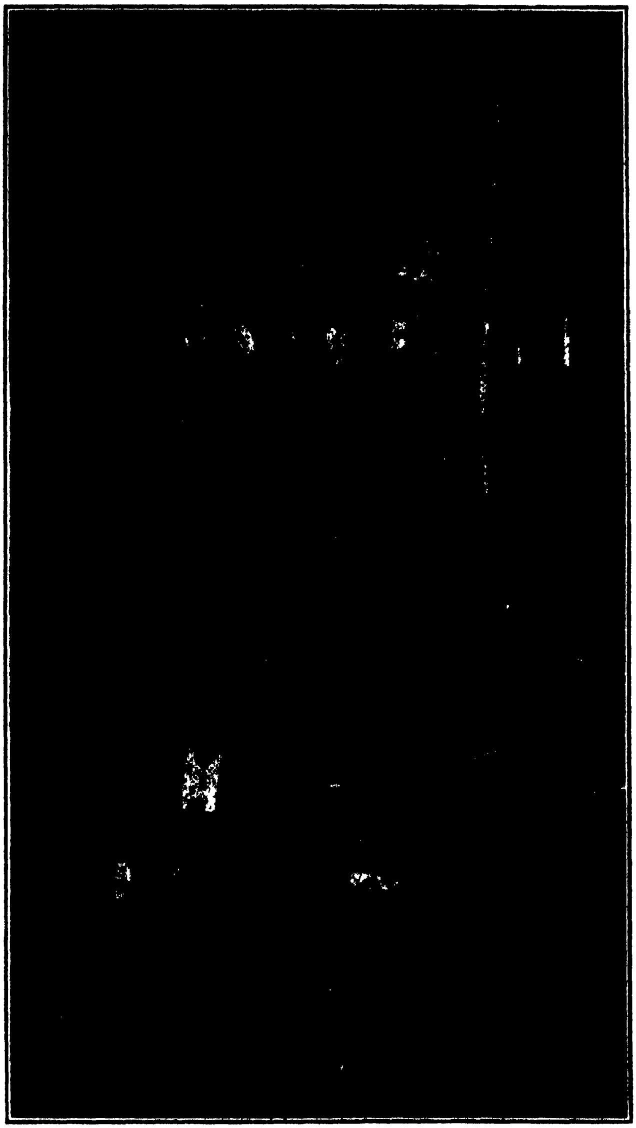

FIG. 5. White pine forest station, showing needle-covered forest floor practically bare of undergrowth. Livingston atmometers on left, Bates evaporimeter on right. Small tree back of Bates evaporimeter is a red spruce; light-barked tree in right background is a red pine; the others are white pine.

The open white pine station (Fig. 6) was placed at the edge of a flat ledge of diorite about 100 feet west of the forest station. It was situated just where the ledge pitches off, above a rather steep slope so as to insure adequate exposure. It received the southwest winds, and winds from the other quarters

FIG. 6. White pine open station. Livingston atmometers and Bates evaporimeter in middle ground in a patch of ground juniper (*Juniperus communis depressa*).

except for trees which cut off part of the force of the north and west winds. The northwest winds came in almost unobstructed. It was somewhat sheltered from the northeast, which was unimportant. The winds reaching this station from the southwest had to pass over the barrier range about a mile away. Not infrequently this station was in the sunlight when the fog was banked up on the mountains and covered the pitch pine station. The sun beat down all day except for 25 degrees above the horizon on the east and 7 degrees on the west.

A considerable portion of the ledge was covered with ground juniper, and the instruments were in a clump of it. There was also a good deal of blueberry. An expanse of bare rock was exposed near the instruments, but to the north so that the wind did not blow over it to the instruments. In all probability it made the readings somewhat higher than they would have been in a similarly exposed open field, just how much it is impossible to say, but certainly not enough to affect the relations between the values for the different types of forest.

Red Oak

The red oak forest selected for study lies in the flat at the eastern foot of Champlain (Newport) Mountain along the road about a quarter of a mile south of where it is crossed by Meadow Brook. The elevation is approxi-

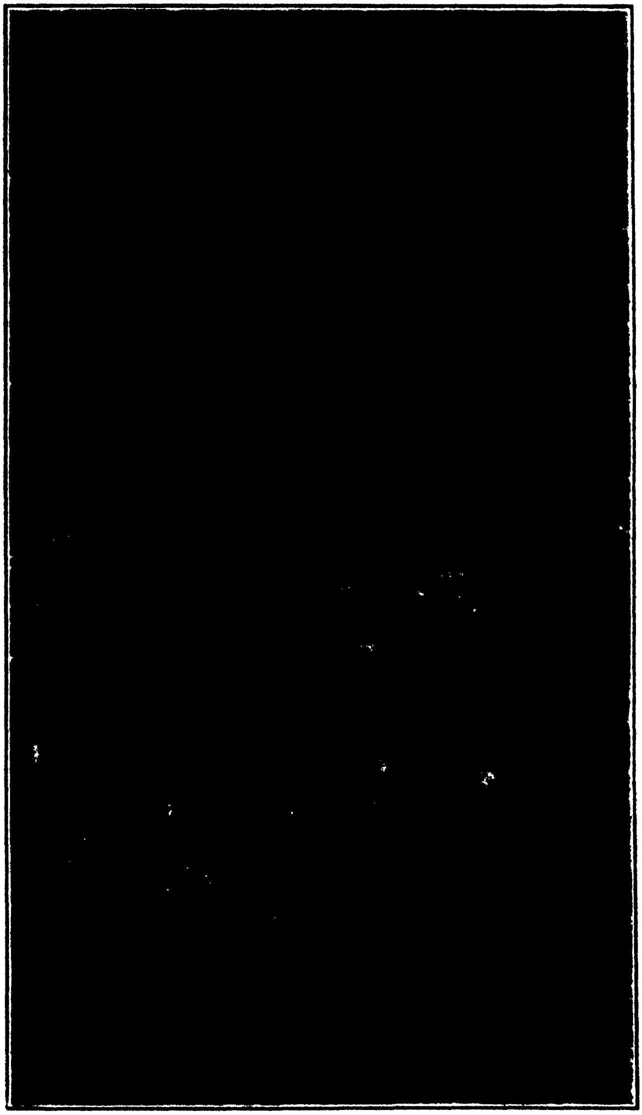

Fig. 7. Red oak forest station, taken within ten feet of evaporimeters. Tree on right is red maple, in middle is shad bush (*Amelanchier canadensis*), on left is red oak. Oak and fir reproduction, and heavy ground cover of asters, wild sarsaparilla and others. Note contrast with white pine forest, Fig. 5, and spruce forest, Fig. 9.

mately 100 feet above sea level. The situation of this flat, lying as it does between the mountain on one side and a low rocky ridge on the other, shows that during the period of submergence it formed a bay sheltered from the sea, almost landlocked. At that time it became filled with silt and mud flats such as we see in similar sheltered bays today. The present soil is, therefore, a very fine silt, quite different from that at the other forest types in which stations were established, and probably of considerable importance as a factor influencing the vegetation. This matter will be discussed more fully below when the soils are considered.

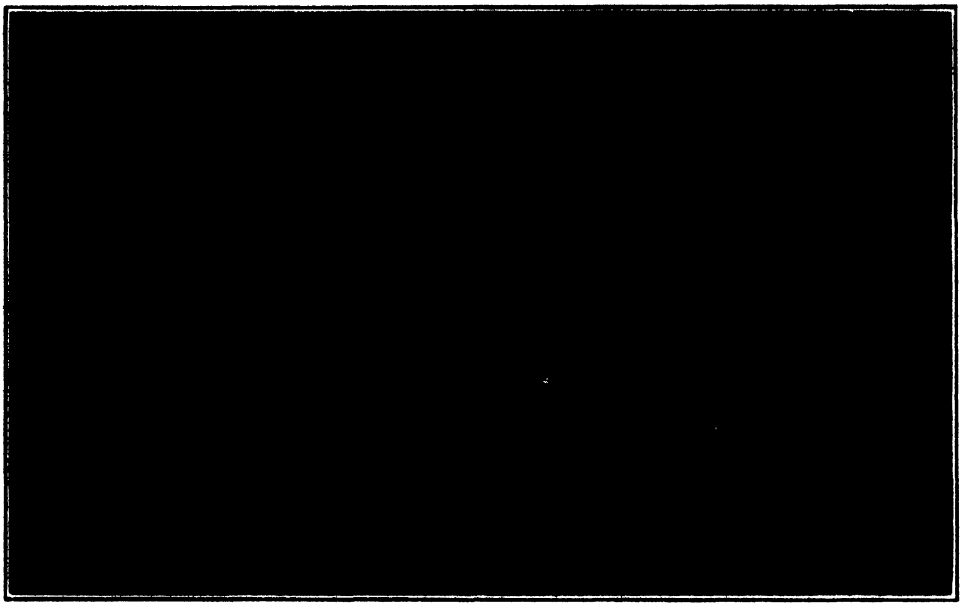

FIG. 8. Red oak open station. Livingston atmometers and Bates evaporimeter.

The particular piece of oak forest in which the instruments were placed (Fig. 7) is only a strip about 200 feet wide between the road and a large open field. The percentage composition of the stand, by actual count of the trees forming the main canopy, was as follows: red oak 51, red maple 25, shad bush, *Amelanchier canadensis* (it reaches tree size here), 9, white birch 5, aspen 4, white spruce 3, balsam fir 2, red spruce 1. The mixture is, therefore, a curious one. Since red oak and red maple together form 76 per cent of the stand, it might more properly be considered an oak-maple type, if there were such a type. The diameter of the oaks, at 4½ feet from the ground, averages 6 inches, ranging from 2 to 10 inches, and their height is from 45 to 50 feet. The maples are a little larger, from 2 to 12 inches, but averaging

only 5 inches, and are the same height. The shad bush runs up to 11 inches in diameter by over 40 feet tall. The stand is approximately even aged, and from 40 to 50 years old. It must have come in after clear cutting, probably followed by fire. The low, and in places swampy, character of the site indicates that it may originally have been a red maple swamp which has gradually dried out, partly through drainage of the adjoining field, permitting the invasion of red oak and other trees which would not grow under swampy conditions. Under the main canopy a second story of hazel, *Corylus rostrata*, covers part of the ground; the instruments were placed by one of these shrubs. The composition of the reproduction, in percentages, is given under the discussion of developmental trends on page 123.

The open location for the oak forest was in a large field which produced rather sparse short hay which did not materially interfere with the instruments (Fig. 8). The poor drainage of the soil was indicated by a carpet of sphagnum moss under the hay. When the grasses intercepted a little wind, they were cut away from the immediate vicinity of the station. There was a full exposure to the south. Winds from the southwest came around and over the shoulder of the mountain. Although the winds did not come so direct as at the pitch pine forest, yet they blew with a good deal of force owing to the position of the open flat between two elevations. The exposure to sunlight was less than for the other types. In the morning the sun had to be 15 degrees above the horizon before striking the instruments, and in the afternoon it set behind Champlain (Newport) Mountain comparatively early, since this elevation extended 23 degrees above the horizon.

Spruce

The spruce forest chosen was on Otter Point about 200 feet south of the road at the end of the "hairpin" turn. It was on a flat about 300 feet back from the sea. The soil was filled with boulders and leached to a grey ashy color for the first 6 inches or more; the boulders occupying as much or more space than the soil. The stand (Fig. 9) was a mixture of red spruce, white spruce and fir, with a little paper birch, the two spruces comprising 69 per cent, the fir 30, and the white birch 1 per cent. The fir was dying out of the mixture, but did not make openings of consequence because the stand was so dense. A spot was selected under the practically complete cover of an approximately even aged growth, of about 40 years, with a forest floor composed of only needles.

The reproduction was 30 per cent spruce and 70 per cent fir, though this does not mean that the fir will predominate in the mature stand, since it dies out rather rapidly.

The open spot chosen to represent the site of the spruce uninfluenced by the forest canopy was above Otter Cliffs (see Fig. 1, station not in picture, but farther back from cliffs). Here almost the only soil seems to be the dis-

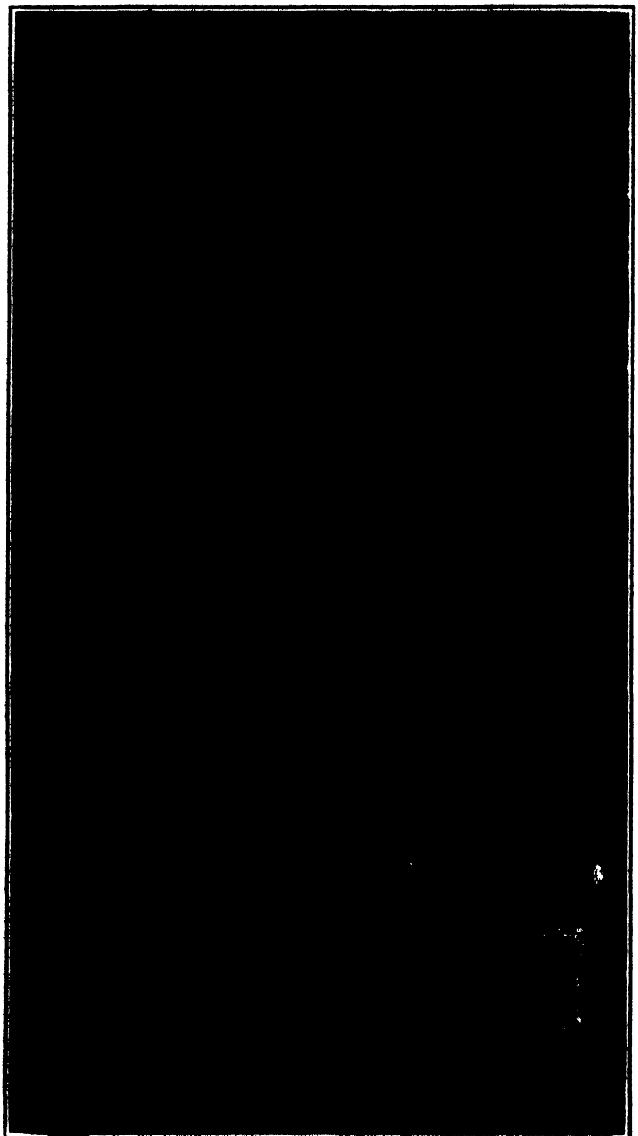

Fig. 9. Spruce forest station, showing density and absence of undergrowth. Livingston atmometers in foreground.

integrated granite in pockets in the ledges. There are some bare rock surfaces, but most of the area is carpeted with crowberry, blueberry, ground-

juniper and other shrubs. The instruments were set in a patch of crowberry near a bare ledge. In depressions were stunted specimens of spruce, white cedar, white pine and white birch. The spot was exposed toward the east and southeast, but sheltered from the southwest, an undesirable but unavoidable feature. There was full sunlight from sunrise until the latter part of the afternoon, when the rising ground and the trees on the west cut off an angle of 23 degrees. After the first week of September 1922, when the site had been studied for nearly two seasons, the instruments were intentionally demolished by unknown persons.* During 1923 a site was selected in an opening which had been cut a year or two before in the spruce forest just north of the road. This opening was about 75 feet in diameter, but received a fair amount of wind and sun.

THE SOILS

There is, over most of the island, rather a sharp differentiation between the surface layer of humus and the underlying mineral soil. The common surface humus, except in the northern hardwoods-spruce type and cedar swamps, is a mat of poorly decomposed needles and litter permeated with fungus mycelium, and usually known as "raw humus" or "duff." Coville calls it "upland peat" to distinguish it from the peat of bogs. Indeed it is more like a peat than a true soil since it contains little or no mineral matter. This humus has already been rather fully described, and its relation to the roots of the more important trees discussed, by one of the authors (Moore, 1922). Suffice it here to say that the humus blanket, where distinct from the mineral soil, contains the bulk of the absorbing rootlets of the trees. This is to be expected since it is the source of most of the nitrogen, as Wherry's analyses, cited below, clearly show. The mineral soil contains the anchorage roots and a small proportion of feeding roots. Owing to the differentiation between the surface humus and mineral soil, and marked differences between the physical and chemical properties of the two, each has been studied separately. The results, as summarized in Table III, show these differences.

The best single measurement of the physical properties of any given soil is the wilting coefficient (Briggs and Shantz, 1912), or line between the available and non-available moisture. It represents the percentage of moisture left in the soil when plants wilt permanently, and is the same for all plants on any given soil. It is, for all practical purposes, a constant determined by the physical properties of the soil. In heavy soils, the percentage of water remaining when plants wilt permanently is high, in light soils it is

* Since they were near the Naval Radio Station, which suffered constant depradations, it is possible that the instruments were mistaken for property of the Navy.

low. The wilting coefficient, therefore, serves as a valuable indication of moisture relations as affected by physical conditions. It also reveals the possibilities of the soil with regard to aeration, since the soil air is controlled largely by physical properties.

The wilting coefficient of the surface humus and underlying mineral soil was determined in each of the four forest types selected for instrumental records. It was also found for a number of samples in the mixed conifer type, in the northern hardwoods-spruce type, and in other examples of the spruce, pitch pine and white pine types.

The direct method, as described by Briggs and Shantz, was followed, using wheat seedlings. Direct determinations are comparatively easy to make and are more accurate than calculations. The surface humus was tested practically as it exists in the forest, except that the larger bits of litter such as sticks, cones, etc., were picked out by hand. A small amount of lime was added on the suggestion of Dr. Shantz, since the high acidity prevented satisfactory growth of the wheat. Although lime changes the physical condition of humus after a certain length of time, it is probable that during the comparatively short period of the tests, and with the small amount used, the error which it introduced was unimportant. With the mineral soils the larger stones and pebbles were picked out by hand. Evidently the stones and gravel in the natural soil influence its physical properties by lowering the wilting coefficient. The exact effect could readily be calculated if necessary. But since the proportion of stones is variable, no useful purpose would be served by such a calculation.

In addition to the wilting coefficient, the moisture holding capacity was determined by the Hilgard (1912, p. 209) method. This is merely the percentage of water which a layer of soil one centimeter thick will hold at saturation. Some difficulty was experienced with the ordinary undecomposed surface humus on account of the slowness with which it took up water because of the large amount of air it contained. Water poured on from above passes through without being absorbed. Some samples remained four days without becoming saturated.

The wilting coefficients and moisture holding capacities of samples of surface humus and mineral soil from the different forest types are given in Table III. These are based on the averages of several determinations, excluding values which were inconsistently high or low. Some of the tests were made on Mt. Desert Island, others in the greenhouses of the Brooklyn Botanic Garden. In general, the tests made at Bar Harbor and Brooklyn gave similar results.

TABLE III. *Wilting coefficients, moisture holding capacities, and acidities of Mt. Desert Island forest soils*

Forest Type	Surface Humus			Mineral Soil		
	Wilting Coeff. Per Cent by Weight	Moisture Holding Capacity. Per Cent by Weight	Specific Acidity. Wherry Scale and pH	Wilting Coeff. Per Cent by Weight	Moisture Holding Capacity. Per Cent by Weight	Specific Acidity. Wherry Scale and pH
SAMPLES FROM INSTRUMENT STATIONS						
Pitch pine	43.2	482	300 (4.5)	6.5	67	10 (6.0)
White pine	39.6	573	300 (4.5)	8.0	65	30 (5.5)
Red oak	31.8	284	100 (5.0)	3.3*	57	3 (6.5)
Spruce	40.2	453	500 (4.2)	1.6	60	100 (5.0)
SAMPLES FROM OTHER FORESTS						
Pitch pine	30.4	—	300 (4.5)	10.2	69	10 (6.0)
White pine	43.9	—	1000 (4.0)	6.1	—	10 (6.0)
Spruce	48.3	—	1000 (4.0)	5.6	55	30 (5.5)
Mixed conifer	38.5	—	300 (4.5)	8.9	—	10 (6.0)
Northern hardwoods-spruce	38.7	—	100 (5.0)	8.8	62	10 (6.0)

* Extraordinarily low for such apparently heavy soil, but agrees with lack of clay.

A glance at the table shows that the wilting coefficients of the surface humus are high. This is because the humus is extremely light, and consequently small amounts of moisture give high percentages by weight. On the basis of volume the wilting coefficients more nearly approach those of the mineral soils. They are: pitch pine humus 8.3 per cent, white pine 7.7 per cent, oak 10.5 per cent, and spruce 7.2 per cent. The more decomposed humus shows a lower wilting coefficient on the basis of weight because it is heavier than the undecomposed raw humus. It is higher on the basis of volume because it is denser. This is shown by the oak humus, which is made up of leaves, and is somewhat better decomposed than the others.

The mineral soils are mostly rather light and porous, as shown by their low wilting coefficients. The extreme lightness of that at the spruce station is due to the fact that it is made up of disintegrated granite. It represents fairly well this type of soil unmixed with humus. The wilting coefficient of 8.0 for the white pine station is somewhat deceptive. This soil is so stony

that it is much lighter and more porous than is indicated by the wilting coefficient of samples from which the coarser stones have been removed. If the stones were included, the wilting coefficient would probably be 4 or lower. The same holds for the other white pine type (Ireson hill) though to a lesser extent.

The low value, 3.3, for the seemingly heavy silt at the red oak is surprising. It is probably due to the lack of colloids, in spite of the fineness of the soil. The value is, however, based on too few determinations for definite conclusions. Some of the tests failed on account of the inability of the wheat seedlings to grow, probably from lack of air due to the density of the soil.

The soil under the canopy of the pitch pine forest where the instruments were located was a pocket of reddish brown glacial till. The values in Table III are from samples of this soil. In other parts of the type the soil is nothing but granite particles mixed with humus, the relatively high wilting coefficient of 10.2 perhaps being due to the humus.

The value of 8.9 for the mixed conifer type does not bring out the variability of the soils on which this type occurs. Samples from ten widely separated locations showed wilting coefficients ranging from 1.8 to 17.6.

Soil acidity was measured by Wherry's colorimetric method (Wherry, 1920), and the values have been inserted in Table III to avoid making an extra table. A large number of additional determinations in various types throughout the island have been secured which are not included in the table.

It has been found that the acidity of the surface humus bears little or no relation to the reaction of the underlying mineral soil. The acidity of the humus is the *effect, not the cause,* of the forest. The surface humus is always acid, the undecomposed humus more highly so than that which is well decomposed, and comes on all types of soil. Thus the forest controls the acidity. This does not mean that acidity is unimportant, for, together with shade and moisture, it determines the character of the vegetation growing on the forest floor.

On the whole, the acidity of the usual undecomposed surface humus throughout the mixed conifer and spruce types, over most of the island, is fairly uniform, running about 300 specific acidity on the Wherry scale (pH 4.5). Not uncommonly it runs up to 1000 (pH 4.0), and is sometimes as high as 3000 (pH 3.5). Specific acidities of 100 (pH 5.0) are usually found in the more open places and burns.

The mineral soil is variable, but usually the reddish brown glacial till has a specific acidity of 10 (pH 6.0), not infrequently running up to 30 (pH 5.5).

and sometimes over 100 (pH 5.0). The ashy grey leached layer is generally between 30 and 100, attaining the higher figures as often or more often than the lower. Both the sands and the clays are low in acidity, around 3 or neutral.

No alkaline soils or rocks have been found except in salt marshes. Wherry reports, however, an alkaline spring flowing into the cedar swamp southeast of Aunt Betty Pond, and another alkaline spring (pH 8.0 specific alkalinity 10) on the east side of Champlain (Newport) Mountain.

The forest which, more than any other, appears to be correlated with the soil reaction is the cedar swamp. The white cedar tolerates high acidity, and its roots have been found in sphagnum with an acidity of as much as 500 on the Wherry scale. But as a rule the substratum of cedar swamps, and of soil in which the cedar is found growing well, is of low acidity or neutral.

On the whole, the results of the acidity tests indicate that, aside from the cedar swamps, the range of acidities found in the mineral soils is insufficient to account for differences in forest types. When the vegetation has become established it creates its own acidity, and may thereby influence the trend of the successional series. Thus for example the spruce, by building up a highly acid surface humus, may create conditions favorable to its own perpetuation, though all the trees on the island seem able to tolerate high acidity.

We are fortunate in having data on soil fertility in the form of analyses which Wherry (1926) made of the nitrates, ammonia and total nitrogen contained in samples from the forest stations included in our study. It would have been interesting to have figures on the nitrification, or nitrate forming capacity, of these soils, a factor which has been shown by Hesselman (1917) to be of the highest importance in controlling the character of the vegetation. The figures which we have on nitrate content do not represent the nitrifying power of the soil because the nitrates may be consumed as rapidly as they are formed, and may fluctuate throughout the growing season. Nevertheless, we know from the work of Hesselman (1917) and of others that nitrates are more important to trees which do not have mycorrhiza on their roots. Mycelium of various fungi, which probably act or may be considered as mycorrhiza, occur on the roots of practically all the trees of Mt. Desert Island, except sometimes on white cedar (*Thuja occidentalis*). In a study of root systems by one of the authors (Moore, 1922) mycorrhiza were found on all species investigated, even beech and sugar maple. However, a more recent investigation of the northern hardwoods-spruce type in the Jordan Pond-Eagle Lake Carry showed that here mycorrhiza are scarce and sometimes lacking on beech and sugar maple, the latter species being particularly free

from them, and are less abundant on spruce and yellow birch than elsewhere on the island. In the northern hardwoods-spruce type the usual distinct surface layer of humus is absent, the leaf mold disintegrating almost as fast as formed, and mixing with the mineral soil. In this type it is probable that the roots are able to obtain nitrates more readily than elsewhere. Over practically all the rest of the island the mycorrhiza appear to be the chief reliance of the trees for obtaining their supply of nitrogen. Threads of fungus mycelium cover the rootlets with a felt-like mat and thoroughly permeate the humus, apparently making the nitrogen of the poorly decomposed "raw" humus available to the rootlets. Hesselman (1917) has found that in this kind of humus, so prevalent in northern regions all over the world, nitrification is very slight or does not occur at all. He considers this due to the high acidity which inhibits the activities of the nitrifying bacteria. It is therefore more than probable that, except possibly in the northern hardwoods-spruce type and white cedar swamps, nitrates play a less important part than total nitrogen. The two latter types comprise hardly more than one per cent of the total forested area (see map). Even on these total nitrogen is a good index of fertility.

Ilvessalo (1923), working in Finnish forests in many respects similar to those on Mt. Desert Island, found a definite correlation between the nitrogen content of the soil and the rate of tree growth. In spite of fluctuations in the individual values, the correlation coefficient was over seven times the probable error. For soluble lime he found also a close correlation; and when the growth increment was compared with the square root of the product of nitrogen and soluble lime, the correlation coefficient was ten times the probable error.

Wherry's nitrogen analyses, while not large in number, are of very great interest for the present study in rounding out our information on the environmental factors in the outstanding forest types of the island. Those analyses which deal with forests considered in this study are presented in Table IV.

One of Wherry's purposes was the determination of the relation between the soil reaction (acidity) and its nitrogen content. His study of soil acidity on the island, and the peculiarities of occurrence of certain plants, led him to think that the influence of soil acidity might be indirect. He arranged his analyses in order of increasing acidity, and this arrangement has been retained in Table IV. There is an evident correlation between acidity and total nitrogen, the nitrogen decreasing in general with increasing acidity.

TABLE IV. *Wherry's nitrogen analyses of soils in forest types of Mt. Desert Island*

HUMUS SOILS

Forest Type	Specific Acidity	Moisture, Per Cent	Nitrogen, Per Cent			
			Nitrate	Ammonia	Total	
					Moist	Dry
* Northern Hardwoods-Spruce	10	79	none	0.200	0.60	2.86
† Red Oak	10	66	0.001	0.005	0.71	2.09
White Cedar Swamp	10	74	0.003	0.005	0.51	1.97
* Hardwoods, N. ridge of Cadillac Mt.	100	58	0.001	0.010	0.57	1.36
† White Pine	315	57	0.001	0.010	0.54	1.24
† Pitch Pine	400	50	none	trace	0.60	1.20
† Spruce	315	48	0.003	0.009	0.54	1.04
* Spruce W. of Eagle Lake	500	40	0.001	0.020	0.52	0.87

MINERAL SOILS AT 20 CM. DEPTH

Forest Type	Specific Acidity	Moisture, Per Cent	Nitrate	Ammonia	Total Moist	Total Dry
* Northern Hardwoods-Spruce	3	30	0.001	0.005	0.16	
* Same, another spot	10	26	none	none	0.07	
* Same, another spot	50	38	none	0.030	0.27	
Av. Northern Hardwoods-Spruce	31	31	0.0003	0.012	0.17	
* Hardwoods, N. ridge of Cadillac Mt.	63	25	none	trace	0.17	
† Red Oak	5	20	none	0.001	0.08	
† White pine	31	30	none	0.001	0.16	
† Pitch Pine	50	35	none	0.003	0.15	
† Spruce	31	17	0.002	trace	0.05	
* Spruce W. of Eagle Lake	200	25	none	none	0.11	

* Station for Bates evaporimeter (see Table VIII).

† Station in regular series for evaporation and soil temperature.

Table IV shows clearly that the nitrogen content of the mineral soil is low, thus explaining the dearth of feeding roots in this type of soil as compared with the surface humus.

Considering first the humus soils, it will be seen that the nitrogen content in the forests bearing deciduous trees and richer under-vegetation is higher than in the coniferous forests except for the hardwoods on the north ridge of Cadillac. The three deciduous forests in Table IV have an average total nitrogen content on the dry basis of 2.10 as against 1.27 for the three coniferous types. Thus the nitrogen of the deciduous forests exceeds that in the coniferous types by 65 per cent.

In the mineral soils, although the total nitrogen is low, the same relationship holds as for the humus. The differences, while not large, are distinct and are in accord with general appearances and the accepted indicator significance of the trees based on agricultural experience.

The important fact which the analyses reveal is that there are distinct differences of soil fertility in the various forest types of the island. A certain part of the differences may be the *effect* rather than the *cause* of the types. But the differences in the nitrogen content of the mineral soils, and their agreements with the humus nitrogen would indicate that the differences of fertility are in the soil itself. This does not mean that the interaction between the forest and the soil should be overlooked.

In the summer of 1925 a further simple soil study was carried out by growing certain plants on samples of soil from the four forests selected for instrumental records and from the northern hardwoods-spruce forest in the carry between Jordan Pond and Eagle Lake. The samples were of mineral soil taken from depths of approximately 18 inches, and were practically free from humus so as to avoid as far as possible the influence of the forest on the soil.

These five different soils were divided into two sets, each of which was further divided into two samples so as to run the tests in duplicate, making 20 samples in all. One set was placed in 7-inch pots, the usual gardener's flower pots, and the other in 4-inch ones.

In the first set was grown golden bantam corn, and in the other red spruce and balsam fir from local seed. The corn was first germinated between moist blotting paper and then transferred to the pots, three plants in some pots and two in others. The spruce and fir seed was sown broadcast directly in the pots, the spruce on one half of the surface and the fir on the other half.

The five soils showed certain marked differences and peculiarities aside from those in the wilting coefficient and other properties above recorded. That from the pitch pine forest, from a pocket in the rock, was a reddish brown loam which was easily brought into a condition of good tilth and maintained so. In fact, its physical properties appeared more favorable than any of the others.

The soil under the spruce, on the other hand, presented certain very unfavorable and seemingly anomalous physical peculiarities. It was a stony or gravelly light yellow sandy loam, but so powdery that when dry the water merely rested on the surface without penetrating, in spite of the large proportion of small stones. When collected it was so dry that water could be introduced only by working it in like some of the so-called instantaneous

cocoa powders. Yet the water so laboriously added dried out more rapidly than with any of the other soils, and every time more was added it lay on the surface a long while before it seeped down. The soil was apparently a glacial till which had been reworked by the sea during the post-glacial subsidence.

The white pine soil was a little darker than that from under the spruce, and more gravelly, but possessed a similar powdery character, though to a much less degree.

The red oak soil was a very fine grey silt, so fine that it behaved very much like clay in sticking together in lumps, and cracking when dry. The presence of a certain amount of clay was shown by the length of time required for settling in water, four days elapsing before the water became clear. Yet water penetrated it very quickly. Before it was placed in the pots this soil was worked by hand into as small lumps as possible. But when water was added these lumps seemed to disappear, and the soil to merge into a rather uniform heavy mass.

The soil from under the northern hardwoods-spruce forest was dark grey and clayey, being lumpy and sticky when wet. It was also worked by hand into as small lumps as possible before being used in the experiment, but, unlike the oak soil, the structure thus given to it was retained. Water added to this soil ran down through almost instantly, more quickly than in any of the others, probably on account of the spaces between the small lumps; yet this soil dried out more slowly than any of the others.

The pots with corn were kept under cover until the young plants had started to grow, when they were placed in the open and protected by wire screens of quarter inch mesh. Those with conifers were kept under cover to prevent the surface drying too rapidly until the seeds had germinated, when they too were put out and protected with wire. When necessary, water was added. After heavy beating rains the soil in the corn pots was cultivated around the plants to overcome the packing which would have interfered with aeration, and to give a dust mulch to conserve moisture. This procedure was of course impossible in the pots with conifers.

The growth in height of each corn plant was measured every five days from June 19 to July 25. The height of the spruce and fir, though not of each individual, was recorded at the same time. On July 25 the corn plants were carefully removed from the soil, and the green weight of the tops and roots determined for each kind of soil.

Considering first the corn, we find that the early differences were due in large measure to the relative rates of germination and early growth. By about July 4, or two weeks after the transfer to the open, differences due to the soil became apparent. The plants on the northern hardwoods-spruce soil,

which on June 19 were among the smallest, surpassed all the others and continued to gain during the remainder of the period until by the end they were markedly larger than those on the other soils. The superiority of the northern hardwoods-spruce soil was amply demonstrated. This is probably due to greater fertility, though it may be due in part to higher moisture holding capacity. The latter is less likely because all soils were occasionally watered, and the pitch pine soil, on which the growth was poorest, showed the best tilth of all.

The height growth on the four remaining soils, the pitch pine, white pine, spruce and oak, does not give a graduated series with well-defined differences between each soil. The average of all the plants on each soil gives virtually the same height for the white pine and oak, namely, 157 and 158 mm. respectively; the pitch pine and spruce were also practically equal, with 130 and 132 mm. respectively. Yet the white pine and spruce soils each had large individual plants, which were larger even than several of the plants on the northern hardwoods-spruce soil, but were counterbalanced in the averages by several small individuals.

On the basis of the green weight of tops, the oak and white pine soils are still equal, with .79 and .78 gram per plant respectively. But the pitch pine soil shows itself to be distinctly inferior to the spruce, with only .46 per plant as against .62 for the spruce soil.

Taking the green weight of the roots and the dry weight of both tops and roots as the criterion, the order of these four soils, the most favorable first, is: oak, white pine, spruce and pitch pine. This agrees with Wherry's nitrogen determinations, which showed the soils under the deciduous forests to contain, on the whole, a higher percentage of nitrogen than those under conifers.

The unfavorable nature of the pitch pine soil, at least for corn, was further shown by the spotting and dying back of the leaves, an effect confined to this soil. Whether this unfavorable condition is due to the presence of toxic substances or to the absence of one or more essential nutrients, it is impossible to say.

With conifers the period was so short in relation to the life of the tree that the experiment affords an indication of only the effect of the different soils on the establishment of reproduction and rate of growth in the earliest stages. Even so, the superiority of the northern hardwoods-spruce soil was just as striking as in the case of corn. On this soil the stand came up more uniformly and thickly than on any of the others. The white pine soil was next best, although markedly behind the northern hardwoods-spruce except that the fir grew taller on it than on the latter. The pitch pine soil came

next to the white pine, there being very little difference between the two. Thus, instead of being at the bottom of the list, as it is with corn, the pitch pine soil is near the top. The red oak and spruce soils both proved very unfavorable to the conifers; the oak soil on account of its compactness, and the spruce on account of its rapid drying. On July 15 everything on both of these soils was dead, in spite of a heavy shower on July 11 and light rain on July 13. The 4 inch pots permitted the soil to dry out too quickly because of their small size. Yet the northern hardwoods-spruce soil in the same sized pots showed very little loss, either because of the greater water holding capacity of this clayey soil or because the roots had grown more rapidly. The white pine and spruce soils lost heavily at this time, but the seedlings on them were not completely wiped out as on the oak and spruce soils.

The favorable showing of the pitch pine soil with the conifers in this short test, as compared with its poor showing with corn, does not necessarily mean that conifers will grow better on it than on the oak soil or spruce soil if once they become established on the latter. It merely means that the good physical condition of the pitch pine soil favored germination and early establishment. The properties which proved harmful to corn might eventually also check the growth of coniferous trees.

TABLE V. *Growth of Red Spruce, Balsam Fir, and Golden Bantam Corn on Soils from five forest types on Mt. Desert Island, Maine*

Soil	Conifers			Corn							
	Height,* mm.			Height, mm.				Green weight per plant, grams		Dry wt. per plant, grams	
	Species	June 29	July 10	June 19	July 4	July 15	July 25	Tops	Roots	Tops	Roots
Pitch Pine	Spruce	9	10								
	Fir	14	18	23	79	100	130	.46	1.16	.062	.26
White Pine	Spruce	11	12								
	Fir	17	18	17	84	123	157	.78	1.77	.105	.345
Spruce	Spruce	8	9								
	Fir	17	18	16	74	102	132	.62	1.47	.068	.28
Red Oak	Spruce	7	8								
	Fir	11	14	22	90	121	158	.79	1.92	.110	.49
N. Hardwoods-Spruce	Spruce	11	12								
	Fir	15	16	17	102	181	215	1.35	2.78	.160	.58

Note: Under height growth, in order to save space, the averages are given for only half of the dates, which however suffices to show the trend and relations.

* Height to base of cotyledons.

The rôle of the soil in the sum total of the environmental factors will be considered below (pp. 83–84) after we have presented the results of the instrumental measurement of certain climatic factors.

INSTRUMENTAL RECORDS OF CLIMATIC FACTORS

The forests of Mount Desert Island lend themselves unusually well to instrumental measurements of their environments. In order to secure comparable records, it is necessary either to use self-recording instruments or to take the readings at the different points simultaneously or practically so. The close proximity of widely different forest types greatly facilitated the readings, and made it possible to get along without self-recording instruments, a fortunate circumstance since such instruments are very costly, and entirely out of reach of the funds which were available for this work.

Factors Measured

It has already been pointed out that the most important environmental influences acting upon plants are related in some way or other to moisture and temperature. We may for the present leave out of consideration light, since it is ample on all sites, except under the forest canopy where it is an *effect,* not a cause of the forest. It was, therefore, desirable to obtain some measure of the moisture and temperature conditions, not necessarily in all their aspects, but something which would serve as an indication of the habitat.

Evaporation was selected as the best single index of moisture conditions practicable to record. The climatic factors which affect evaporation also affect the plant, though not in the same way. The critical function of the plant is transpiration, or giving off water through the leaves. The quantity transpired may be from approximately 300 to over 1000 times the weight of the dry matter produced. When the rate of loss from transpiration exceeds the rate at which water reaches the leaves from the stem and roots, the plant wilts and eventually dies. Evaporation increases with decreasing relative humidity, with increasing temperature, with wind and with sunlight. Hence in measuring evaporation we obtain a combined measure of these important factors. The difficulty is that, while evaporation responds to these factors in a definite way following known physical laws, transpiration does not. Since transpiration depends upon the reaction of a living system to external forces, it is much more complex than evaporation. Plants tend to decrease their rate of transpiration with increasing evaporation, and thereby to a certain extent protect themselves against unfavorable influences. We may, therefore, consider evaporation as a good measure of the conditions to which the plant is

subjected, but not of the water loss of the plant itself. This is important to bear in mind, since there is a natural tendency to think of the water given off by an evaporating instrument as bearing a closer relation to that given off by the plant than it really does. However, it is a good indication of what the plant is undergoing, and of the stresses to which it must adapt itself if it is to survive.

There are a number of instruments for measuring evaporation, each of which responds differently to the various forces acting upon it. The type generally used in studies of vegetation and its environment is the Livingston (1915) porous cup atmometer. This instrument was selected because it gives readings which can be compared with those taken by other investigators in various parts of the country, and because of certain advantages in manipulation. Since the instrument has been described in readily accessible articles it is sufficient to say that the evaporating surface is a porous sphere about twice the size of a golf ball, which is connected by glass tubing with a reservoir bottle from which the water is drawn up as rapidly as it evaporates from the surface of the sphere. Readings are taken by measuring with a burette the amount of water required to refill the reservoir. Distilled water only was used. A mercury valve prevented the entrance of rain water while permitting the outgo of water for evaporation.* The Livingston atmometer has two main drawbacks. First, it is extremely sensitive to wind, and therefore tends to give too high readings on windy sites. Transpiration is also affected by wind, but not nearly so markedly as the Livingston spheres. Secondly, it is very easily broken by frost. A comparatively light freeze on September 20, 1921, broke both spheres in the open station for the red oak forest.

During 1921 and 1922 a set of Bates (1919) inner cell evaporimeters was read simultaneously with the Livingston atmometers at the four open stations. The instruments were not in good working order in 1921, but were improved in 1922. During 1923 and 1924 the Bates instruments were very useful in extending our knowledge of evaporation to forests not included in the series of four stations. The rate of water loss from the Bates evaporimeter is much less than that of the Livingston atmometer for the same rate of atmospheric evaporation, enabling readings to be made less frequently if desired, a great convenience with isolated stations. From a purely mechanical point of view the Bates instrument, being all metal, withstands more rough usage, and is not injured by the frost, a serious drawback of the porous porcelain

* During the first season, 1921, the ordinary glass wool and mercury seal was used. During 1922 and 1923, Musch tubes (see Nichols, 1923) were employed. Though subject to certain disadvantages, their greater ease of manipulation rendered them more satisfactory for our purpose than the glass wool seal. See, however, Thone, 1924.

spheres in cold climates. When the surface of the Bates evaporimeter is blackened, as it usually is, it absorbs the heat of the sun and gives a combined record of evaporation and insolation. This may be desirable in some cases but in others the result is a tendency to mask the true conditions. The readings in this particular instance afford a good example: the greater insolation at the white pine station, as compared with pitch pine, counterbalanced the lower evaporation, so that the readings for the two stations were practically the same (see page 68). To measure evaporation alone, it would probably be better to leave the original polished metal surface, or to paint it white. The principal drawback of the Bates instrument is that different environmental conditions affect it differently, so that it does not give as consistent readings as the Livingston. This prevents the construction of satisfactory curves of current evaporation throughout the season. But it is to a certain extent overcome in the averages for the season when different evaporimeters are run at the different stations in regular rotation. A further disadvantage is the necessity for taking the readings by weighing.

Readings were taken weekly, all stations being read on the same day. The readings could not be made at the same hour, but the difference due to the different time of day is not large enough to introduce an appreciable error in the total amount evaporated during the week.

A rough measure of solar radiation was obtained by running Livingston black atmometers alongside of the white ones, and taking the difference between the two. The higher evaporation of the black sphere is due to heating by the sun, hence it affords a rough measure of insolation. In fact a pair of white and black porous cups is known as a " radio atmometer " and has been used as such by Burns (1923). It has been shown by Briggs and Shantz (1916) that solar radiation " may be looked upon as the primary causative factor in the cyclic changes " (changes throughout the 24 hour period). The transpiration of plants follows the curve of radiation more closely than that of evaporation or temperature. The correlation coefficients of transpiration with radiation range from .82 to .89, with temperature from .77 to .86, and with relative humidity from .75 to .85.

The readings of solar radiation were not altogether satisfactory because the black porous spheres had not been quite perfected. With very intense rates of evaporation, such as not infrequently occurred at the open pitch pine station, water was not delivered to the surface of the sphere rapidly enough, and the readings were too low. Under the forest canopy a spot of sun may strike one sphere and not the other. Eventually, however, the errors from this source tend to compensate one another. While the instruments do not

give precise records of solar radiation, they can be used for general indications when their limitations are understood.

The temperature relations were studied by recording soil temperature. Two depths were selected, 6 inches and 18 inches, under the forest in each of the four types studied. These two depths represent fairly well the soil layers occupied by tree roots on Mt. Desert Island: the former gives conditions encountered by the seedlings and by the feeding roots of the larger trees, the latter represents the conditions for most of the anchorage roots, since the trees of the island are as a rule rather shallow rooted.

Both maximum and minimum thermometers were placed at each depth in each type near the atmometers, and were read weekly at the same time as the atmometers. Thus each reading gives the warmest and coldest temperature of the soil for the entire week. The soil temperature work was started a year later than that on evaporation, and the records cover the summers of 1922 and 1923. Obtaining the maximum temperatures offered no special difficulties because the thermometers could be placed upright in wooden tubes sunk in the ground to the desired depth. It was, however, necessary to artificially cool the thermometer after reading and before setting back. But the minimum readings involved the problem of keeping the thermometer in a nearly horizontal position in the soil, something which had not yet been done in this kind of work. The difficulty was met by constructing wooden boxes 2 by 14 inches (inside measurement) and the desired depths. Into these boxes the thermometers were lowered on a string attached to a separate loop of string fastened at each end of the instrument. This device permitted the raising and lowering of the thermometers without tipping, an important matter, since errors due to shifting of the plunger by tipping are very common.*

The similarity between the pitch pine forest of Mt. Desert Island and the same type on Long Island has already been mentioned. Mt. Desert Island is near the northern limit of this forest as a distinct type or association. Long Island is near its optimum. Obviously, simultaneous measurements of conditions in pitch pine on Long Island and Mt. Desert Island would be of considerable interest in revealing something of the range of conditions under which the type can grow. Accordingly, a spot was selected in the pitch pine forest of Long Island, at Coram, near the middle of the island. Here stations

* Since our work was completed, Toumey and Stickel (1925) have tested various methods of measuring soil temperature, including the above. They found that our soil boxes gave readings which deviated somewhat from standard soil thermometers and from thermometers similar to ours exposed in a way they devised. The differences however seem to compensate, and do not materially detract from the results given below.

were set up in 1921 in the open and in the forest for measuring evaporation. During the summer of 1921 the importance of synchronous readings between Long Island and Mt. Desert Island was not realized, so the periods are not all comparable. But the results are, nevertheless, extremely interesting. During 1922 and 1923 the readings were made on the same days in the two places, and thermometers were installed for recording soil temperature at 6 and 18 inches. Evaporation readings in a hardwood forest on Long Island, and on Montauk Point, taken at the same time have given additional interesting results, which will be dealt with more in detail in a publication on the vegetation of Long Island, but which will be touched upon briefly below, on account of some rather striking and unexpected comparisons.

Results

General. The summers of 1921, 1922 and 1923 happened by good fortune to show marked contrasts in moisture. That of 1921 was unusually dry and warm. There were long periods without precipitation, during which drought conditions were severe. In the first drought, which lasted from early June until about the middle of July, a good many tree seedlings, even 5 years and older, wilted and died. This gave an excellent opportunity for determining the differences between the evaporation in the different forest types during critical periods.

The summer of 1922, on the other hand, was unusually wet on Mt. Desert Island, but not on Long Island. There was hardly a week that the Mt. Desert readings were not taken in the rain. This season gave a comparison of evaporation during a period favorable to the forests on all sites. The summer of 1923 was again very dry. The droughts were not as prolonged as during 1921, but the evaporation during dry periods reached even higher levels.

Evaporation. The rates of evaporation for the four forest types during the summer of 1922 are shown graphically in figures 10 and 11. The curves for 1921 and 1923, while having different values, show essentially the same form and relationship between the four types, so need not be reproduced. The averages for the season are shown at the right. The average for the pitch pine forest on Long Island, New York, has been added, for comparison.

Table VI presents the averages for each of the three seasons. The weekly readings are not included since they would take up an undue amount of tabular space.* The table shows under the average for each station the relative rate or ratio based on the pitch pine station as 100. These ratios

* The authors will gladly furnish copies of the weekly readings to anyone who wishes them, at cost of reproduction.

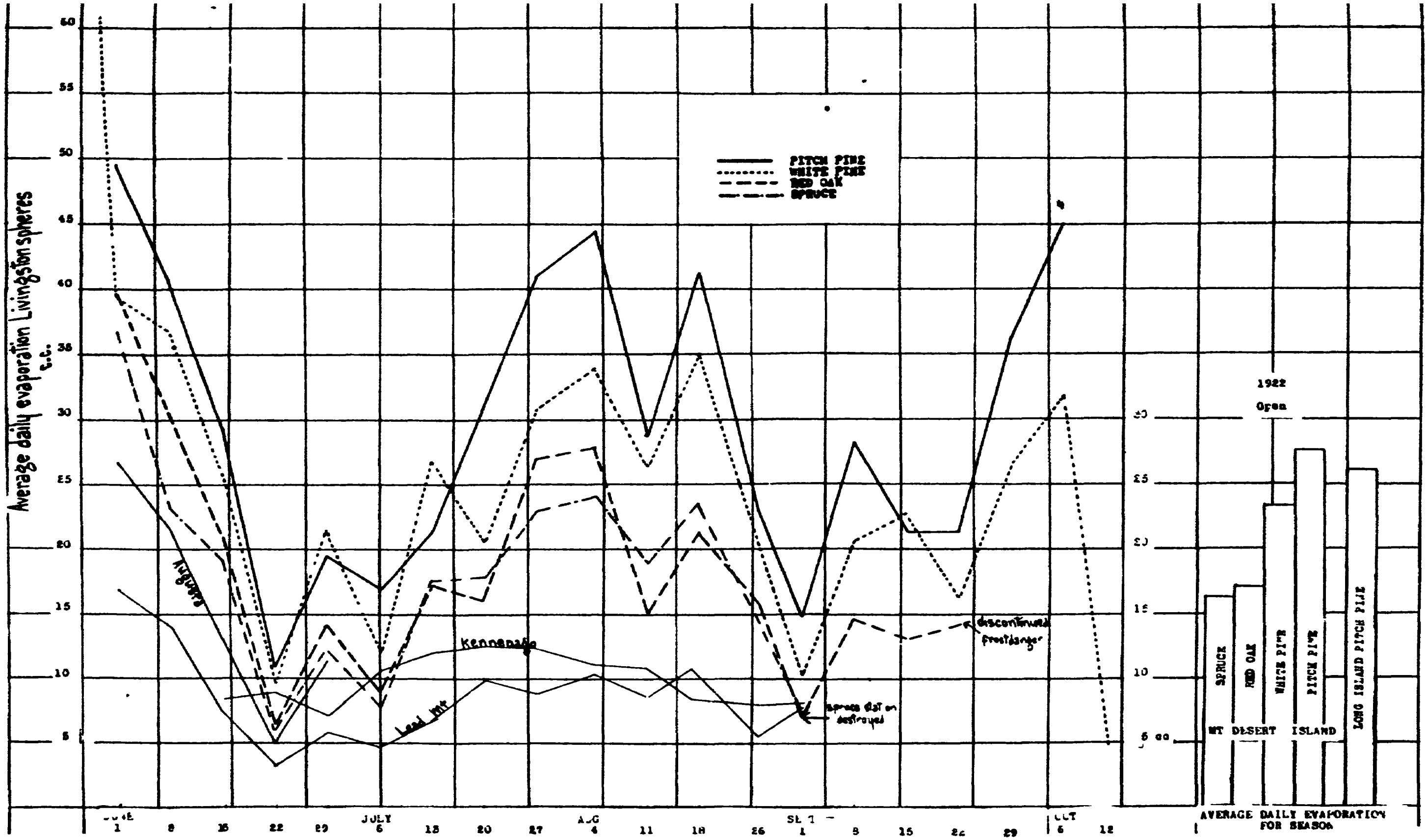

FIG. 10. Graphs showing the course of evaporation at the four open stations in 1922. Livingston white atmometers, average daily reading for each period in cubic centimeters of water evaporated. The dates along the bottom are those on which the readings were taken, not the dates of the vertical lines which represent ten day intervals.

Curves for three inland stations, Kennebago, Lead Mt. and Augusta, during the earlier part of the season have been added for comparison. On right the daily averages for the entire season are shown graphically, and Long Island added.

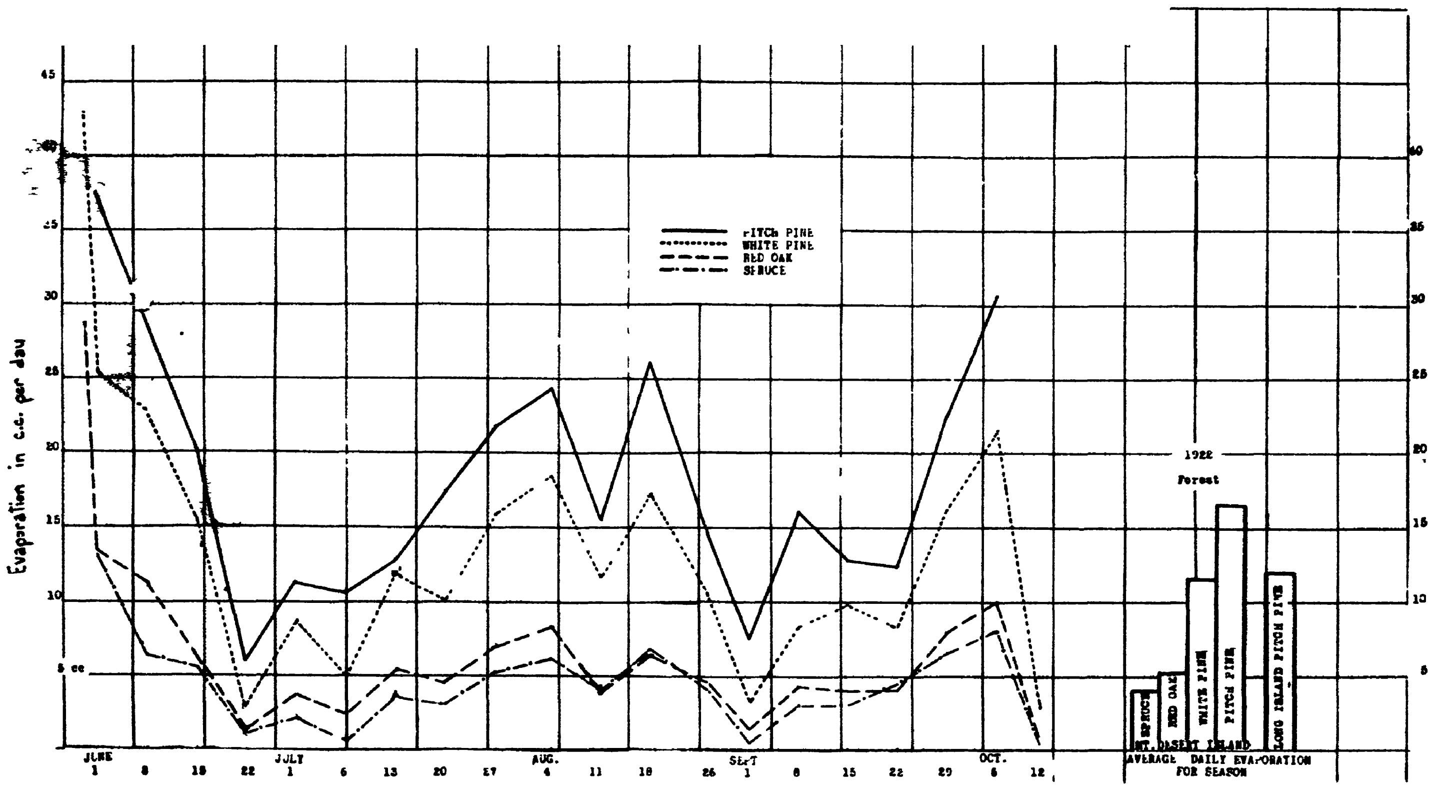

FIG. 11. Graphs showing the course of evaporation at the four forest stations in 1922. Livingston white atmometers, average daily reading for each period in cubic centimeters of water evaporated. Daily averages for the entire season shown graphically on the right.

give a quantitative measure of the relations of the types to each other so far as evaporation is concerned.

The tables and figures bring out some exceedingly interesting relationships. The open stations, it should be remembered, represent the actual conditions of the site, uninfluenced by the forest canopy, that is, the conditions which the forest has to overcome to establish itself. The rates at the pitch pine and white pine stations are admittedly high on account of the heating of the rock ledges surrounding the instruments. But the young pitch pines at the pitch pine station, and young white pines at the white pine station, are successfully encountering these conditions.

Whether the conditions at the stations selected are more severe or more favorable than in the same forest type elsewhere on the island it is impossible to say, except in the case of spruce, which had a lower rate of evaporation than the spruce forest in the interior of the island, as will be pointed out below (pp. 69, 70).

TABLE VI. *Average daily evaporation (in cubic centimeters) from Livingston white atmometers at four forest types, in the open and under the canopy, on Mt. Desert Island, Maine, and at a pitch pine forest on Long Island, New York. Figures in parentheses show relation to Mt. Desert pitch pine.*
1921, 1922 and 1923

	Open					Forest				
	Long Island	Mt. Desert Island				Long Island	Mt. Desert Island			
	Pitch Pine	Pitch Pine	White Pine	Red Oak	Spruce	Pitch Pine	Pitch Pine	White Pine	Red Oak	Spruce
1921 evaporation ..	21.8	32.0	25.0	24.5	18.6	9.0	24.6	16.1	9.4	6.8
	(68)	(100)	(78)	(77)	(58)	(37)	(100)	(65)	(38)	(28)
1922 evaporation ..	26.2	27.7	23.4	17.2	16.4*	11.9	16.6	11.6	5.3	4.0
	(95)	(100)	(84)	(62)	(59)	(72)	(100)	(70)	(32)	(24)
1923 evaporation ..	22.1	37.3	30.7	24.7	21.4†	12.1	24.3	17.4	8.5	7.0
	(59)	(100)	(82)	(67)	(57)	(50)	(100)	(72)	(35)	(29)

Periods covered. Mt. Desert Island: 1921, June 13 to Sept. 24; 1922, May 30 to Sept. 22; 1923, June 9 to Sept. 28, all inclusive. Long Island: 1921, June 14 to Sept. 25; 1922, June 1 to Sept. 22; 1923, June 29 to Sept. 28.

* Last 3 weeks interpolated from curve. Station destroyed.

† In different location from 1921 and 1922, artificial opening in forest not exposed to sea.

Table VI shows at a glance that there are fairly sharp and definite differences in the four Mt. Desert forests. These differences are all the more

noteworthy in view of the results secured by the New York Botanical Garden in the hemlock type (Moore, Richards, Gleason and Stout, 1924), which showed a striking similarity between the rates of evaporation under hemlock forests in widely separated localities. Our differences between different types a few miles from each other are far greater than the New York Botanical Garden found in examples of the same type three hundred miles apart.

It is significant that the relative order, from the highest to the lowest, is the same in the open as under the forests, and is consistently maintained throughout the season, as well as in all of the three years. This is ample evidence that the differences are not accidental or due to occasional combinations of climatic conditions, but are real and consistent. The differences, or spread between the extremes, is accentuated by the forest cover. Thus under the forest the evaporation for the lowest (spruce) is only about one quarter of that for the highest (pitch pine); while in the open the spruce is a little over half of the pitch pine.

The very much higher rate at the pitch pine than at the spruce, and intermediate rates for red oak and white pine, are what one would expect from general appearances. Observations would lead one to anticipate very dry conditions in pitch pine, less dry conditions in white pine, a good degree of moisture in red oak, and possibly even more moisture in spruce. However, it would have been difficult by observation alone to have distinguished between the atmospheric moisture conditions of the red oak and spruce. Thus the relations agree with developmental stages of succession from open and drier to moister and denser types. The red oak, though, is not a usual stage in the series. These relations are more fully discussed below. Suffice it here to say that, with such a very high rate of evaporation at the open pitch pine station, it is doubtful if the stages of succession can be carried very much further so long as the present physiographic conditions continue. The slope will have to become less precipitous, less exposed, and covered with more soil. Evidently, this is a matter of many centuries, so that for all practical purposes the pitch pine at this place may be considered a physiographic climax.

The comparative rates of evaporation of the pitch pine, white pine and spruce correspond with the geographic position which these types represent. The type from the most southerly region of the three, the pitch pine, has the greatest evaporation; the most northerly region, the spruce, has the lowest, with white pine in between. Red oak is not representative of another region, and has the next lowest rate. The low evaporation of the Long Island pitch pine, or rather the high rates of the Mt. Desert as compared with Long Island,

brings up an interesting and important question which will be discussed under the interpretation of the instrumental data.

The rate of evaporation varies a good deal throughout the summer. But there seems to be a general similarity between the different years. Three periods of high evaporation appear to be characteristic. The first comes in June, in the early part of the month in 1922 and 1923. The records do not cover May, but it is generally rather moist. The second comes early in August in all three years, sometimes starting at the end of July. The third high period, though considerably less than the June and August ones, occurs in early September. In 1923 there was only a slight rise at this time, and the really dry part of the third high period did not come until September 21st.

The differences between the four forests are not the same throughout the season. In very moist periods the rates all fall, and come closer together. The rest of the time, even in the intermediate periods, the differences are marked. The rise and fall in rate, from week to week, is frequently parallel for all the stations. Sometimes, however, one rises or falls more sharply than the others. Occasionally one falls while the others rise, or *vice versa*. This is probably due partly to the direction of the wind. All stations except the spruce were exposed to the prevailing southwest winds in the manner already described. But a wind from the northwest was cut off more at the pitch pine than at the other stations.

It is interesting that the graphs of the different stations cross each other only a comparatively small number of times. During 1922, the spruce and oak openings ran so close together that they occasionally crossed, the rate at the spruce sometimes exceeding that at the oak. During 1921 the oak and the white pine ran fairly close together and sometimes crossed. Under the forest there was practically no crossing at all, each station maintaining its relative position consistently throughout. Yet the differences between the oak and spruce were often very small.

The averages of the readings of evaporation secured with the Bates evaporimeters during the season of 1922 are given in Table VII. Since the spruce station was destroyed, after September first, we have given the averages from June 1 to September 1 in addition to those from June 1 to September 22 in which the last three weeks at the spruce station have been interpolated. The longer period shows lower values because the September rates were lower than earlier in the season, as would be expected, and bring down the average. The ratio to pitch pine as 100, based on the longer period, has also been added for comparison. The ratio for the shorter period is practically the same.

TABLE VII. *Average daily evaporation at open stations for 1922, by Bates evaporimeters, in cubic centimeters*

	Pitch Pine	White Pine	Red Oak	Spruce
June 1 to Spetember 1..........	7.09	7.16	6.17	5.24
June 1 to September 22..........	6.73	6.72	5.68	4.86*
Ratio to Pitch Pine June 1–Sept. 22.	100	100	84	72

* Interpolated from September 2 to 22, after the instrument was destroyed.

It will be noticed at once that, with the Bates evaporimeters, the white pine rate equals that of the pitch pine. It has already been explained on page 60 that the Bates instrument, on account of its blackened surface, records insolation as well as evaporation but does not separate the two as do the Livingston black and white atmometers. As will be shown below, the solar radiation, or insolation, at the white pine open station was markedly higher than at the pitch pine. This counterbalances the lower white pine evaporation, and makes the results of the combined evaporation and insolation, as given with the Bates instrument, practically equal. Thus, if we had used only these instruments we would not have known that the pitch pine evaporation is considerably higher than that for the white pine, while the insolation is lower.

During 1922, as will be seen from Table IX, the solar radiation at all other stations was higher than at the pitch pine. Consequently the ratio of the other stations to pitch pine is higher with the Bates instruments than with the Livingston ones. Nevertheless, the order of the stations, aside from the higher position of the white pine due to its high insolation, is the same as that given by the Livingston atmometers. The results confirm those already given in Table VI.

This is the first time, so far as we know, that Livingston and Bates instruments for measuring evaporation have been run side by side for an entire season in an actual study of vegetation. The results, therefore, afford a fairly reliable basis for an estimate of the relative merits and uses of these two rather different kinds of instrument.*

* The open pan, although it has sufficient advantages over other methods of measuring evaporation to warrant its adoption by the Weather Bureau as the standard, would be useless for weekly readings because rain would introduce an error which could be corrected only by running a rain gauge alongside and calculating the amount which fell into the pan. In this particular case we had no rain gauges.

For short period studies, the open pan, unless it is very shallow, does not give a true picture of the course of evaporation throughout the day because of the length of time it

Bates evaporimeters were used also in 1923 and 1924 to obtain a rough comparison between the rate of evaporation at the four stations and in some of the more interesting forest types in other parts of the island. During 1923 the object was principally a comparison of the spruce station at Otter Point and a representative spruce forest in the interior of the island, west of Eagle Lake, and of the red oak station with a hardwood forest containing spruce in mixture on the north ridge of Cadillac (Green) Mountain. The composition of this hardwood forest was as follows: beech 44 per cent, red maple 13, white birch 13, red oak 10, yellow birch 8, sugar maple 4, spruce 4, hornbeam (*Ostrya virginiana*) 4. The reproduction above the small seedling stages had a considerably larger proportion of spruce than the main canopy. A comparison was also secured between the white pine station and the spruce forest west of Eagle Lake.

During 1924 the object of the Bates readings was to learn something of the rate of evaporation in two very interesting examples of virgin forest, the northern hardwoods-spruce in the carry between Jordan Pond and Eagle Lake (described below on pages 127–128) and the spruce on Western Mountain. The latter is a stand of pure spruce at an elevation of approximately 650 to 700 feet, characterized by a luxuriant carpet of moss about 4 inches deep on a thick blanket of humus covering the rock. There seems to be little or no soil below the humus, as so often happens in the true spruce slope type. Reproduction of spruce is abundant and thrifty.

The records for both 1923 and 1924 are given in Table VIII. It is clear that the spruce forest in the cold shore zone has a lower rate of evaporation than the same type in the interior of the island, lower even than the virgin spruce on Western Mountain. The hardwoods on the north ridge of Cadillac (Green) Mountain have a lower rate than the red oak station, which the Livingston records have shown to be a decidedly moist forest. It is interesting that the hardwood forest has a little less evaporation than the spruce forest west of Eagle Lake. In 1924 the first set of readings showed a remarkable similarity in the evaporation of the cold shore spruce, the virgin northern hardwoods-spruce, and virgin spruce of Western Mountain. In the second and longer period all three of these forests showed low rates of evaporation, but the differences between them were distinct. That the Otter

takes for the water to warm up. But for less intensive studies, where the total for the season is the principal desideratum, it is possible that the Weather Bureau standard pan run alongside of a rain gauge might make a satisfactory combination. A drawback for studies in out-of-the-way places, which are often of interest to the botanist, is interference by thirsty animals or bathing birds, which are less of a factor around human habitations where the Weather Bureau stations are generally located.

Point spruce should be the lowest was to be expected, but the difference between the northern hardwoods-spruce and the pure spruce of Western Mountain is greater than had been anticipated. A part of this difference is perhaps due in this case to greater light under the spruce than under the hardwoods, since the spruce is on a mountain top while the hardwoods are in a narrow valley; furthermore the canopy in the former is somewhat more open, as indicated by the abundant reproduction and luxuriant moss. The Bates evaporimeters, as already pointed out, give evaporation and insolation combined. The indications from these figures, considering the two years, are that a climax deciduous forest has a little lower rate of evaporation than a climax coniferous forest, except where the latter is on a distinctly colder site.

TABLE VIII. *Evaporation under forests not included in the series of stations, compared with that under the stations. Bates evaporimeters, in c.c. per day, 1923 and 1924*

1923	
June 15 to July 19, 34 days	
Spruce station, Otter Point	1.84
Spruce west of Eagle Lake	2.40
Red Oak station, Meadow Brook	2.49
Hardwoods, north ridge of Cadillac (Green) Mountain	2.14
July 21 to August 14, 24 days	
Spruce west of Eagle Lake	1.89
Hardwoods, north ridge of Cadillac (Green) Mountain	1.76
August 14 to September 29, 46 days	
Spruce west of Eagle Lake	1.71
White pine station	2.41
1924	
June 8 to July 27, 48 days	
Spruce station, Otter Point	1.70
Spruce on Western Mountain	1.85
Northern hardwoods-spruce of Jordan-Eagle carry	1.85
July 27 to September 20, 55 days	
Spruce station, Otter Point	.53
Spruce on Western Mountain	1.25*
Northern hardwoods-spruce of Jordan-Eagle carry	.82

* In a different part of the forest from the June 28–July 27 readings.

Solar Radiation. The drawbacks of the Livingston black and white porous spheres, or radio atm meters, for measuring insolation have already been pointed out (p. 60). However, after making due allowance for the crudity of the method, the results are worth a moment's consideration. The figures for the three seasons, 1921, 1922 and 1923, are presented in Table IX, to-

gether with the averages for the three years, and ratio on the basis of pitch pine as 100.

TABLE IX. *Average daily solar radiation, or difference between Livingston black and white atmometers, for 1921, 1922 and 1923, in cubic centimeters*

	Open				Forest			
	Pitch Pine	White Pine	Red Oak	Spruce	Pitch Pine	White Pine	Red Oak	Spruce
1921 June 12 to Sept. 24 . . .	8.29	11.58	7.50	9.57	3.21	.26	.59	.40
1922 May 29 to Sept. 22	5.74	8.75	9.73	7.80*	1.41	.84	1.15	.50
1923 June 4 to Sept. 21 . . .	8.12†	10.96	8.33	5.74‡	2.49	1.58	1.13	.70
Average of 3 seasons . . .	7.24	10.01	8.57	7.70	2.34	.90	.97	.53
Ratio to Pitch Pine . .	100	140	118	106	100	38	41	27

* To September 1, only.

† From June 29.

‡ Lower than preceding years for spruce because of the different location of the station. A larger proportion of sunlight was cut off by the trees surrounding the opening.

The records show that the pitch pine station has a markedly lower insolation than the white pine, in spite of its higher evaporation. This is easily explained by the fogs which, as already pointed out, sometimes blanketed the pitch pine station while the white pine was in sunlight. These solar radiation figures, therefore, give us a very rough quantitative measure of the difference in sunshine between the parts of the island to the north and to the south of the barrier range. It is interesting that one habitat may be very much drier than another a short distance away, yet not subject to as high insolation.

The differences in solar radiation between the four open stations are due not only to different proportions of sunshine on the northern, as compared with the southern parts of the island, but to topographic features which cut off the sun during a certain proportion of the day, which proportion differs at the different stations. The hilly character of the island, which gives such a variety of sites, causes also variation in the proportion of total sunlight in different places. We have not worked out this proportion for the different stations, since we are interested primarily in the actual conditions. But measurements of the horizon angle indicate that the percentage of sunlight cut off by the hills adjacent to the pitch pine forest is not much greater than the percentage cut off by trees near the white pine station.

Under the forest the solar radiation is reduced by the crown canopy. If the insolation were the same at all open stations, the values for the forest stations would be a good measure of the crown density. Nevertheless, in spite of the differences at the different open stations, the shade which the

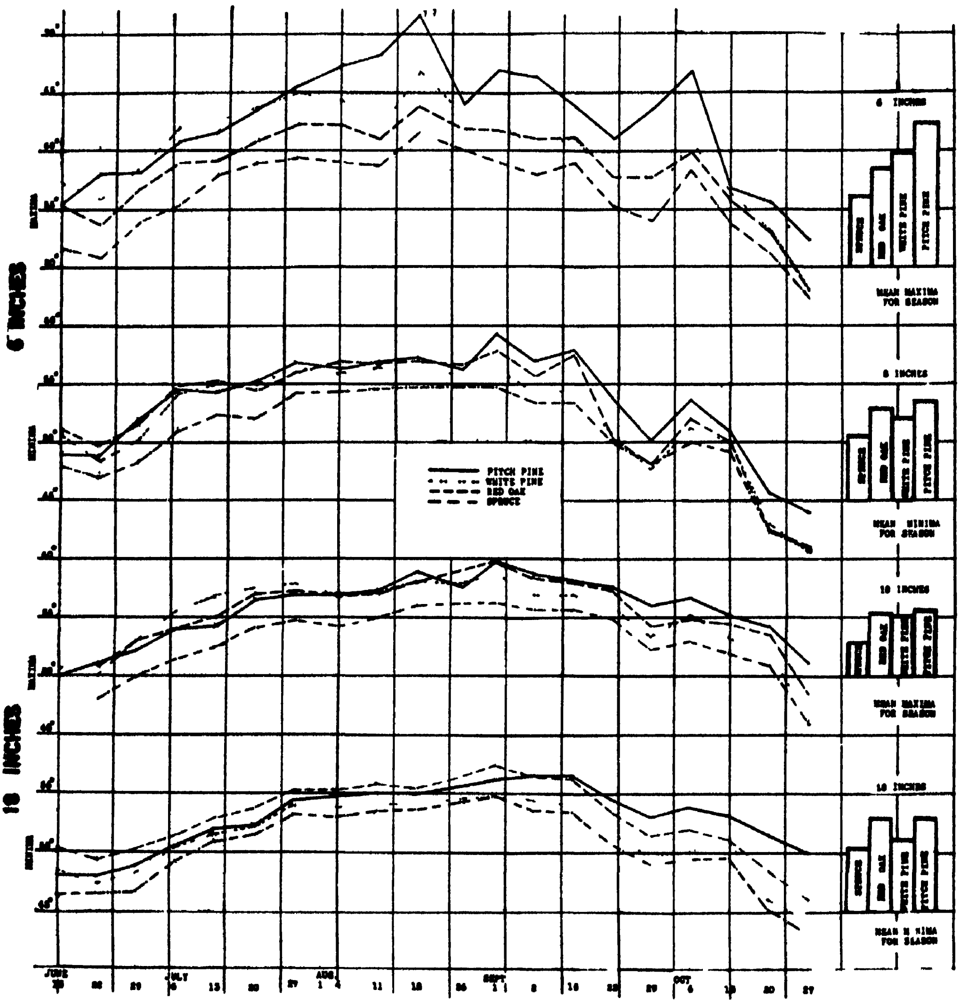

FIG 12. Graphs showing the course of soil temperature at the four forest stations in 1922 Maxima and minima at 6 inches and 18 inches depth in degrees Fahrenheit. On right the averages for the entire season are shown graphically

trees themselves cast exe- - so much influence that the values are roughly in proportion to the canopy. It will be noticed that pitch pine is more than twice as high as any of the other stations in spite of its lower insolation in the open. This is unquestionably due to the open character of the forest, at

though the instruments were under a group of trees. The very low value of the spruce station reflects the well-known density of this forest type. White pine and oak were intermediate. The oak forest had a more open canopy than the white pine, but this was counteracted to a certain extent by the understory of hazel and other shrubs.

Soil Temperature. The marked difference between the moisture conditions of 1922 and 1923 has already been mentioned. We should suppose that 1922, being much moister than 1923, would also be cooler. If it was, the soil temperature does not show it, or only very slightly. When the records have been reduced to corresponding periods for the two years, June 15 to October 5, 17 weeks, the similarity is extremely close, as Table X shows.

TABLE X. *Comparison of Average Soil Temperature, in degrees F., at 6 and 18 inch depths, for corresponding periods, June 15 to October 5, for 1922 and 1923 on Mt. Desert Island*

	6 inches				18 inches			
	Pitch Pine	White Pine	Red Oak	Spruce	Pitch Pine	White Pine	Red Oak	Spruce
1922	59.2	57.2	56.9	54.5	54.7	53.8	54.8	52.3
1923	60.4	57.7	57.4	54.9	53.7	53.0	53.6	51.5

It will be seen that there is less than one degree of difference between the two years in most of the types of forest. This is the more interesting in that it was entirely unsuspected, and was not realized till the readings had all been averaged. It is curious that at 6 inches the year 1923 is a trifle warmer than 1922, probably because of the drier conditions in 1923, but at 18 inches 1923 is a trifle cooler, perhaps an after effect of the winter.

The similarity between the two years 1922 and 1923 holds not only for the averages shown in the foregoing table, but also for the maximum and minimum temperatures. Furthermore, the relationship between the four forest types is the same in both years.

The readings have been plotted in such a way as to bring out differences between the four forest types at 6 inches and 18 inches. To avoid confusion, the maxima, minima and means were plotted separately for each level. This gives six graphs for each year, or twelve in all. In view of the similarity just noted, only enough graphs to show the general form, and certain interesting indications, have been reproduced as figures 12 and 13. The figures also show graphically the averages for the season in order to bring out the re-

lationships between the soil temperatures of the different forests for the whole season. Table XI gives the mean maxima and minima, as well as the averages at 6 and 18 inches for 1922 and 1923. As with evaporation, the weekly readings have been omitted to save space.

TABLE XI. *Soil temperatures (in degrees F.) under four forest types on Mt. Desert Island, Maine, at 6 inches and 18 inches in depth*

	6 Inches Depth				18 Inches Depth			
	Pitch Pine	White Pine	Red Oak	Spruce	Pitch Pine	White Pine	Red Oak	Spruce
1922								
Av. Maxima	62.4	59.8	58.5	56.2	55.7	55.0	55.3	52.8
Relation to pitch pine	(100)	(96)	(94)	(90)	(100)	(99)	(99)	(95)
Av. Minima	53.5	52.1	52.8	50.6	53.0	51.2	52.9	50.4
Relation to pitch pine	(100)	(97)	(99)	(95)	(100)	(97)	(99)	(95)
Means	58.0	56.0	55.7	53.4	54.4	53.1	54.1	51.6
Relation to pitch pine	(100)	(97)	(96)	(92)	(100)	(98)	(99)	(95)
1923								
Av. Maxima	66.7	62.6	61.4	58.3	54.9	54.4	54.5	52.3
Relation to pitch pine	(100)	(94)	(92)	(87)	(100)	(99)	(99)	(95)
Av. Minima	53.6	52.6	53.2	50.9	51.8	50.9	52.4	50.1
Relation to pitch pine	(100)	(98)	(99)	(95)	(100)	(98)	(101)	(97)
Means	60.2	57.6	57.3	54.6	53.4	52.7	53.5	51.2
Relation to pitch pine	(100)	(96)	(95)	(91)	(100)	(99)	(100)	(96)

Periods: For 1922, June 9 to October 27, 20 weeks.
For 1923, June 2 to October 5, 18 weeks.

In the maximum temperatures at six inches the relationship between the four types of forest is the same as was found with evaporation (see page 65).

The 6 inch minima as a whole run very much closer together than the maxima. Probably they are of less importance in growth than the maxima because they merely indicate how cold it gets—a negative condition—while the maxima give positive conditions, and afford some conception, though rough, of the amount of heat available for growth.

In the minimum temperatures at 6 inches the order of the stations is changed. Although the spruce is still the lowest, and pitch pine the highest,

the white pine drops below the red oak. In fact the red oak is very little colder than the pitch pine until the end of the season, as the curves show.

At 18 inches, the differences between the forests are much less than at 6 inches. Apparently as we go deeper we approach the general temperature of the island which here and there is altered on the surface by certain conditions of exposure to the sun, of winds, moisture and so forth.

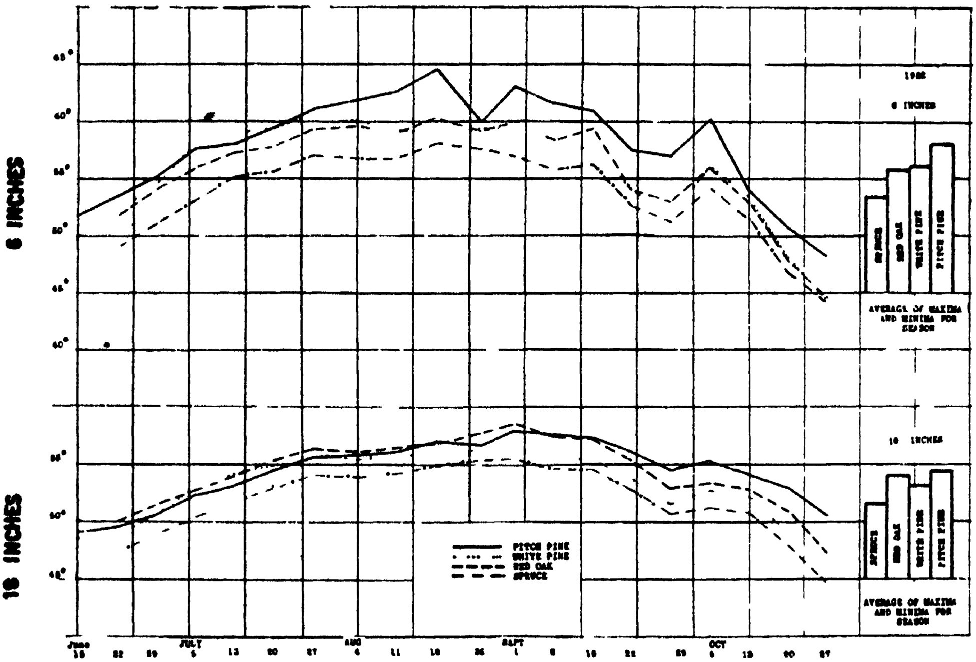

FIG. 13. Graphs showing the course of soil temperature at the four forest stations in 1922. Means $\left(\frac{\text{Maximum} + \text{minimum}}{2}\right)$ at 6 and 18 inch depths in degrees Fahrenheit. On right, the averages for the entire season are shown graphically

The 18 inch temperatures bring out a relationship between the four forest types which is different from that which was found at 6 inches. Spruce still remains undisputably the coldest. White pine is still intermediate between the spruce and pitch pine, so that the relations between these three important types are the same. But red oak rises unexpectedly, and challenges the position of pitch pine. In fact, in the minima and means for 1923 it slightly surpassed the pitch pine. This comes about because the red oak maxima are practically as high as under the pitch pine, and the minima are consistently higher than at the other stations, until the latter part of the season, when the pitch pine shows both higher maxima and minima. The graph of the 18 inch

minimum for 1922 clearly shows the higher temperature of the red oak till September 8, and higher pitch pine temperature from then on to October 27. This relationship balances in the average minimum for the season, so that there is only .1 of a degree difference in favor of the pitch pine. In 1923 the same relationship holds, almost to a day. But the readings did not extend so late into the period when the pitch pine was warmer, so that in the average for the season the red oak surpasses the pitch pine by .6 of a degree.

It is worth while noticing that the temperatures in the pitch pine, both at 6 and 18 inches, and in both years, tend to fall less rapidly in the autumn than they do in the other forests. All the curves show a distinct prolongation of warmer conditions under the pitch pine as compared with the other types.

Fluctuations in soil temperature are, of course, important, since they necessitate changes in the rates at which the internal processes of the plant are carried on. In general, the less the fluctuation the easier it is for the plant. The difference between the maximum and minimum readings for the week gives us the range of the extreme fluctuation. The difference between the mean maximum and mean minimum gives the mean fluctuation. This is presented in Table XII.

TABLE XII. *Average fluctuations in temperature (differences between maxima and minima in degrees F.) in four Mt. Desert Island forests, 1922 and 1923*

	6 Inches				18 Inches			
	Pitch Pine	White Pine	Red Oak	Spruce	Pitch Pine	White Pine	Red Oak	Spruce
1922								
Fluctuation	8.9	7.7	5.7	5.6	2.7	3.8	2.4	2.4
Relation to pitch pine	(100)	(87)	(64)	(63)	(100)	(141)	(90)	(90)
1923								
Fluctuation	13.1	10.0	8.2	7.4	3.1	3.5	2.1	2.2
Relation to pitch pine	(100)	(76)	(63)	(56)	(100)	(113)	(68)	(71)

Periods: 1922, June 9 to October 27;
1923, June 2 to October 5.

It will be seen that for the 6 inch depth the order in which the forest types stand with regard to temperature fluctuations is the same as with evaporation and six inch soil temperature. A part, but not all, of the greater fluctuation under pitch pine is no doubt due to the more open canopy.

On the whole, the fluctuations, even at 6 inches, are comparatively small

when we consider that they represent averages of the spread for the entire week. At 18 inches they are so little as to be of slight importance. Here the white pine has a wider spread than any of the others, no doubt on account of its lighter soil.

During wet periods the 18 inch depths at the red oak and pitch pine became flooded. At the former station it was due to the low situation, at the pitch pine to the fact that the soil was in a pocket of rock which probably filled up with water from the slope above. It does not seem, however, that this materially affected the soil temperature, since of course the water would have the same temperature as the soil.

It is interesting to compare the soil temperatures of the pitch pine type on Mt. Desert Island with those for the same type on Long Island. Since the records for the latter cover a shorter period than the former, the Mt. Desert averages have been worked out for the same period as those included for Long Island. The results are given below in Table XIII. The thermometers at 18 inches were set up in a different way on Long Island which may have given readings relatively a little higher.

TABLE XIII. *Soil temperatures (in degrees F.) in pitch pine forests on Mt. Desert Island, Maine, and Long Island, N. Y., 1922 and 1923*

	6 Inches						18 Inches					
	Average Maxima		Average Minima		Means		Average Maxima		Average Minima		Means	
	Mt. Des.	Long I.	Mt. Des.	Long I.	Mt. Des.	Long I.	Mt. Des.	Long I.	Mt. Des.	Long I.	Mt. Des.	Long I.
1922 June 22–Oct. 6 (16 wks.)	64.2	74.6	55.0	59.3	59.6	67.0	56.5	71.6	53.6	58.0	55.0	64.8
1923 June 29–Sept. 28 (14 wks.)	67.3	72.1	54.2	62.9	60.7	67.5	55.7	68.8	52.7	64.2	54.2	66.5
Fluctuations (Max.-Min.) 1922					9.2	15.3					2.9	13.6
1923					13.1	9.2					3.0	4.4

It will be seen that the Long Island pitch pine grows under higher temperatures than that on Mt. Desert Island. The 6 inch maxima are 9.6 degrees higher in 1922, but only 4.8 degrees higher in 1923. The 6 inch means are 7.4 and 6.8 degrees higher in 1922 and 1923 respectively. These differences,

in spite of the widely different geographical locations, are only a little more than those between the different types within 3 miles of each other on Mt. Desert Island. At 18 inches the mean differences were more marked, 9.8 in 1922, and 12.3 in 1923. The 6 inch fluctuations, or spread between the maxima and minima, were higher on Long Island in 1922, and on Mt. Desert Island in 1923.

INTERPRETATION

The most unexpected and difficult to explain of the various results of the instrumental records is the extremely high rate of evaporation on Mt. Desert Island as compared with Long Island. The Mt. Desert rate is also much higher than inland in Maine, as shown by records taken by the Forest Commissioner of Maine in 1922 (see Fig. 10). If there is anything which one would have thought could be depended upon, it is that the evaporation on the Maine Coast must be lower than on Long Island. Evaporation is controlled by temperature, by relative humidity of the air, or rather by vapor pressure, and by wind movement. Mt. Desert Island is much colder than Long Island; the vapor pressure for the nearest Weather Bureau Station (Eastport) shows it to be somewhat lower, but not enough to counterbalance the higher Long Island temperature. Lastly, wind movement is less on Mt. Desert Island than on Long Island. Montauk Point on Long Island is near Block Island, the windiest point on our Atlantic Coast. In fact, the wind on Montauk is so strong that, so far as can be determined, it is the chief cause of the failure of the downs to become forested. Yet the evaporation on Montauk Point, in that strong wind, and with a fairly high temperature, was *less* than on Mt. Desert Island with its moderate winds and coolness. It is indeed a surprising phenomenon. Only in a wet year, 1922, does the Long Island pitch pine evaporation even approach that of Mt. Desert Island. In other years even the spruce on Mt. Desert almost equals the Long Island pitch pine.

There is no questioning the instruments. The records for the three years, and for the different stations, both on Mt. Desert Island and on Long Island, all agree. There must evidently be some explanation. It is unnecessary to go into the various comparisons which were made of the factors controlling evaporation. The only Weather Bureau data available had been collected at some distance from our forest stations, and therefore did not show the specialized local conditions responsible for the seeming contradiction.

Ultimately, with the assistance of Dr. C. F. Marvin, Chief of the Weather Bureau, we have developed an hypothesis which appears reasonable. In a word, the high evaporation of Mt. Desert Island seems to be due to the interaction of the surrounding cold sea water and sun-heated granite hills.

The prevailing winds in summer are from the southwest. When these winds pass over the sea off Cape Cod they are moderately warm and moist. When they reach the Gulf of Maine they are cooled, and their capacity for holding moisture is correspondingly reduced. The cooling frequently reaches the point at which the moisture condenses in the form of fog. Hence the frequent fogs along that part of the Maine Coast in summer. Sometimes the fog is carried from the sea onto the island, but often it lies off shore. It is a common sight, standing on the Mt. Desert hills in the blazing sun, to look out to the fog banks resting on the sea. Therefore the southwest wind, by the time it reaches the island, has lost much of its moisture. The island heats up in the sun more than the usual land mass because of the considerable surface of rock which reaches high temperatures under the intense insolation. The cool air from the sea, on striking the island, becomes warmed, and its relative humidity correspondingly lowered. Thus the southwest wind off the cold sea becomes in reality a very dry wind as soon as it reaches the island, and gives the high rate of evaporation which our instruments revealed.

The wind, continuing inland, picks up moisture rapidly from the transpiring forests and other vegetation, and from the numerous lakes. Hence the rate of evaporation a short distance inland is lower than on the coast. This is contrary to what we should expect, but is the inevitable result of the cold waters of the Gulf of Maine.

The high rates of evaporation are, however, frequently interrupted by exceedingly low rates. On cloudy days the winds are not warmed so much in passing over the island, and may have a high degree of humidity. Sometimes the fog bank pushes in from the sea and completely covers the island. Thus we have both very high and very low evaporation, the net result of which is nevertheless an extraordinarily high average rate for this latitude and general climate.

The high evaporation and dry though cool air probably explain certain characteristics of the Mt. Desert Island climate which have long been common knowledge among persons living on the island, and have had much to do with its popularity in summer. There is no question but that the climate exerts a stimulating effect similar in certain ways to that of mountainous regions. With nervous persons it sometimes causes sleeplessness. The principal features of mountain climates, aside from the rarefied air, are coolness and high evaporation, just the features which are found on Mt. Desert Island. Here the mountain stimulus can be enjoyed without the attendant disadvantages of the rarefied air.

The instrumental records show that there are marked differences between the moisture conditions of the sites of the four forest types studied, differ-

ences not created by the forest itself. The records show distinct but not large differences in soil temperature which may to a certain extent be influenced by the forest canopy. While soil temperatures in the open would, of course, be higher than under the forest, we are inclined to think that the order of the stations would be the same, just as with evaporation the order under the forest was the same as in the open.

On the whole, we had expected somewhat larger differences in soil temperature between forests representative of regions so far apart as New Jersey and Labrador, that is, between the pitch pine and the spruce. The differences recorded by us are considerably less than Shreve (1924) found between north and south exposures at the same elevation in the Arizona Mountains. Yet he concluded that the temperatures which he found were less important than moisture.

One might be tempted to infer that temperature is unimportant as compared with moisture. But our figures lend themselves equally well to the opposite deduction, namely that rather small differences in temperature are of much significance. It would be well, therefore, to withhold judgment on this point. For the present we can say that pitch pine on Mt. Desert Island grows on drier and warmer sites than any of the other forest types measured, that spruce grows on the wettest and coldest, while white pine comes next to pitch pine, and red oak next to white pine in these two respects.

It has already been pointed out that the south side of the island as a whole is cooler and moister than the north side, and receives a larger proportion of fog. Yet, where abrupt south facing rocky slopes occur on the southern side, the intensity of the insolation overcomes the effects of the fogs, and results in warmer and drier sites than those which receive less fog north of the barrier range. The pitch pine station on Huguenot Head is a notable example of such exception. Observation shows a preponderance of spruce on the southern as compared with the northern half of the island, and also in a fringe or zone close to the sea all around the island.

Fortunately, our spruce station was in this coastal zone so that no doubt is left as to its cause. It is both colder and moister than the interior of the island. Hence we have called it the cold coastal zone. Unquestionably within this zone spruce is the climax forest type. In this respect it corresponds to the upper slopes of the Adirondack Mountains, White Mountains, and Maine, above the belt of beech, yellow birch and sugar maple. These upper slopes, known to fore ers as the "spruce slope type," are clothed with spruce on account of their climate, which in turn is due to their altitude. They are colder than the hardwood ridges below, and possibly also more moist. On Mt. Desert Island, in the coastal fringe, the cold is due to the

proximity of the cold sea water instead of to altitude; but the result is almost the same.

There are, however, breaks in the coastal zone. A striking example is the pitch pine forest growing almost to the water's edge along the Ocean Drive on the cliff just south of the Satterlee Sand beach. How can this be reconciled with the pitch pine type as inhabiting the sites with the highest evaporation and warmest soil temperature? We have already shown that the bare rock heats in the sun and causes a sharp decrease in the relative humidity of the air passing over it. Apparently this dryness in some cases overcomes the influence of the proximity of the cold water. There may be another factor at work in the case of the pitch pine forest along the Ocean Drive. The prevailing southwest winds which strike this forest have come over the land. Thus it is possible that at least part of the time this spot is subjected to conditions typical of locations inside of the cold coastal zone. The same may be true of other breaks in the zone. Whether or not certain localities along the shore are subjected to overland winds, the bare rock itself is a powerful factor in modifying conditions. The plants typical of warmer regions which we found in the coastal zone were always on or near an exposure of rock.

Averages give but an imperfect picture of environmental conditions as they affect plants; the maximum and minimum conditions which go to make up the average are the critical ones. The figures for average daily evaporation throughout the season must, therefore, be considered in the light of the high and low rates which they include. The seasonal averages of 32.0, 27.7 and 37.3 c.c. per day include considerable periods when the pitch pine station was covered with fog, and the evaporation zero. The highest weekly rate at this station was a total of 393.5 c.c., or 56.1 c.c. per day from July 6 to 13, 1923. During that summer there were four times when the totals for the week exceeded 360 c.c., two of these times they were nearly 380. Unfortunately, we have few records for single days. But in a comparison between the regular pitch pine station on Huguenot Head (Pickett) and Acadia (Robinson) Mountains near a stand of scrub oak (*Quercus ilicifolia*) the pitch pine open station lost 64.4 c.c. from 7 A.M. to 7 P.M. (see p. 106). Undoubtedly on some days the evaporation here has been still higher. Thus the atmospheric conditions on this slope at times approach those of the semi-arid mountains of Arizona and New Mexico. It is probably safe to say that pitch pine occupies the south facing slopes of Huguenot Head (Pickett) because the evaporation is too great to permit the existence of other trees. Soil moisture may also be a limiting factor. But the only soil moisture data which we secured, in September, 1921, after a three weeks' drought which

should represent critical conditions rather well, showed the soil under the pitch pine to have about as much available moisture as in the three other forest types.

Thus the pitch pine forest is on Mt. Desert Island in the first place owing to a chain of circumstances in the geological past, the principal feature of which was the extension of the coastal plain above water from Cape Cod to Newfoundland. It is now confined to the drier, and also probably warmer, sites where it is not subjected to serious competition. On these sites the soil is thin or lacking, and such of it as occurs in pockets was found in one case at least to be very infertile.

The occurrence of white pine is to be attributed to conditions less dry than those endured by pitch pine, but drier than would be congenial to spruce, as well as to soil conditions, which will be discussed more fully below.

The red oak type is not considered as fitting into the series of four stations as a representative of a more or less distinct forest region. Nor does it constitute a usual stage in the successional series up to the climax forest of the island. From the point of view of moisture relations, the type is intermediate between the white pine and the spruce. In 1921 the evaporation at the open station almost equalled that for the open white pine station; in 1922, the moist year, it only slightly exceeded that for spruce; while in 1923 it was more nearly midway between, though still nearer to the spruce. It is reasonable, therefore, to think of the red oak evaporation as more or less typical of that prevailing over the rest of the island between the sites on which white pine flourishes and those on which spruce predominates. This includes the larger part of the island.

With regard to temperature conditions, the red oak type presents certain peculiarities which may or may not be of importance. The soil temperature at 6 inches places it in the same relation to the other types as did the evaporation. It comes, however, somewhat nearer the white pine than the spruce. This is in accordance with what has just been said concerning its relation to the remainder of the island, since the spruce station is typical of the cold zone bordering the sea. The red oak temperature, therefore, is probably fairly representative of the rest of the island which, as would be expected, is a little cooler than the white pine type and distinctly colder than the pitch pine.

The soil temperature data agree in placing the four forest types in the same order with regard to warmth as with regard to evaporation. Warmth and dryness seem to go together. Yet they also indicate that below the surface—18 inches is not very deep—the soil temperature on Mt. Desert Island back from the cold shore zone is nearly the same, even on widely different

sites. This temperature, which appears to be about the same from year to year, is low, approximately 54° F.

Applying the foregoing to the island as a whole, the forest types may be arranged in the order of dryness and warmth, the driest and warmest first, as follows: pitch pine, white pine, mixed conifer and spruce. The northern hardwoods-spruce is moister than the spruce type in the interior of the island, but drier and probably also warmer than the spruce of the cold shore zone.

In placing the forest types of the island in a regular order with regard to climate, we do not imply that the conditions which prevail in any given type are permanent. In some cases, as for example the pitch pine forest on Huguenot Head (Pickett Mountain), the conditions are so unfavorable and will change so slowly that the type may for all practical purposes be considered permanent. But elsewhere the conditions change progressively. They are ameliorated by the vegetation itself in such a way that evaporation is lowered and it becomes possible for a type requiring lower evaporation to succeed the one which has endured the severer conditions. The manner in which this takes place is described below under the Developmental Trends of the Vegetation.

Thus far we have been considering only the interpretation of the forest types in the light of the instrumental records of climatic factors, mainly moisture and temperature. Let us for a moment turn our attention to soils, and endeavor to see how much influence the soil has upon the occurrence of the different types. Obviously, each type is the resultant of climate and soil acting together, and in turn acted upon and modified by the forest itself.

Wherry's analyses of soil nitrogen, presented above in Table IV on page 53, showed that the soils on which the deciduous forest types grow are more fertile than those bearing coniferous forests. The northern hardwoods-spruce type is caused partly by more fertile soil, as shown by the culture tests of 1925, described above under Soils (pp. 54–57), and partly by more favorable moisture due to its advantageous topographic situation. It is also not unlikely that the shelter which it enjoys from the winds directly off the sea may also be a favoring factor; in general the type is not found on the mainland before we reach a distance of about 20 miles or more from the coast, while in the interior it is the dominant type.

The spruce type appears to be determined more largely by climatic than by soil factors, and is probably the climax or ultimate type of vegetation on all but the more fertile and moister soils or sheltered positions. It can grow on soils poor in nitrogen, and probably also low in other nutrients, once other plants have prepared the site and built up sufficient humus.

The white pine type is temporary, and sure to be crowded out by the

spruce, though a certain proportion of scattering pines may remain on the drier sites. The evidence on this island, as well as elsewhere in New England, points to the physical properties of the soil as being of importance in determining the establishment of the white pine. Abundant soil aeration and good drainage, characteristics of light or porous soils, seem to be required. In central New England the tree will seed in and occupy abandoned fields on heavier soils, but is unable to maintain itself there more than one generation owing to the competition of broadleaf trees. On the lighter soils, reasonable care in cutting generally ensures its perpetuation by natural reproduction.

The limited occurrence of the white pine as a type on the island (see map) may be attributed largely to the limited area of sufficiently porous soil, and its practical exclusion from the cold shore zone to the climate. The abundance of the tree scattered over the island is accounted for by locally favorable conditions of soil aeration and fertility due to rock or stony soils and humus accumulation, and to the favorable climate away from the proximity of the sea. It may be noted that the tree is much more plentiful on that part of the island north of the barrier range which has already been shown to be somewhat less cold and less subject to fogs. No doubt also the open character of the forest in many places, due to cutting, has favored the reproduction of white pine and increased its numbers over what they were in the virgin forest.

The pitch pine type has already been shown to be confined to the drier and warmer sites on which evaporation seems to be too high for the other trees. These sites are very largely ledge rock with only a thin layer of granite particles, and here and there pockets of glacial till which the culture tests of 1925 have shown to be sometimes very infertile. This type is therefore due to both climatic and soil factors, probably more largely the former. It does not occur on rock ledges which are not dry and hot.

The red oak type is probably very largely a soil response, since none of the climatic factors are such as to preclude the establishment of the spruce forest. The mineral soil, in spite of its low nitrogen content, .08 per cent, and heavy character, seems to possess at least a fair degree of fertility, if we may judge by the culture tests of 1925. It is probable also that the very fine texture of the soil, by preventing sufficient aeration, excludes the conifers but not the red oak and red maple. It is well known that the latter grow on heavier soils than the spruces and pines. As humus accumulates and improves aeration of the so.., the spruce comes in and crowds out the oak. This explains the greater abundance of spruce in the understory as compared with the main canopy, brought out by our tree counts in this type.

Vegetation as an ever changing, living thing has already been emphasized. Changes go on until a stage of equilibrium is reached.* This represents the highest type which the particular climate and soil can produce—the climax association. Under the free play of natural forces any given set of climatic conditions produces a *climatic climax,* except where soil conditions, such as infertility, prevent the attainment of the climax, when we have a *physiographic climax,* sometimes also called an edaphic climax. When a physiographic climax is due to infertility of the soil, it is permanent. When, however, as in the case of the pitch pine discussed above, it is due to physiographic conditions which will improve in the course of centuries, the physiographic climax is not truly permanent though it may be considered so for all practical purposes. In reality, it is an arrested climax, or lower stage held fixed by physiographic conditions which change very slowly.

The series of stages, or successional series, through which vegetation passes before attaining the climax, are commonly divided for convenience on the basis of the kind of site on which they originate. Thus we have series starting on dry sites, such as rock, known as xerarch series (controlled by dry conditions); series starting in water, such as ponds or lakes, known as hydrarch series (controlled by water); and all intermediate series, such as ordinary soils, known as mesarch series. Vegetation may start at the opposite poles so far as moisture is concerned, and yet reach the same climax.

When a successional series has been thrown back to a lower stage by interference, such as fire or lumbering, and starts over again, it is known as a *secondary* successional series. Since most of Mt. Desert Island has been burned or logged over at one time or another, most of the series are secondary. When the interference has wiped out the vegetation and even the surface humus, as in the case of a severe fire, the series goes all the way back to the original starting point, and becomes practically indistinguishable from a primary series. The numerous expanses of bare rock on the island, and historical records of large mature trees where we now find rock ledges, show that this has sometimes happened.

The accompanying chart (Fig. 14) shows what appear to us to be the chief lines of succession on the island. Each series does not necessarily pass through all the stages given on the chart. There is sometimes a certain

* Actually, complete equilibrium is probably seldom or never attained.

amount of "telescoping," that is, a stage may be skipped. For example, on the Western Peaks there are places where, after a severe fire, spruce comes in directly without the intermediate birch-aspen stage. Obviously it is impracticable to represent all these cases on the chart, and the full series has been shown. Only in certain conspicuous instances, like pitch pine on the light soils series, the telescoping has been indicated.

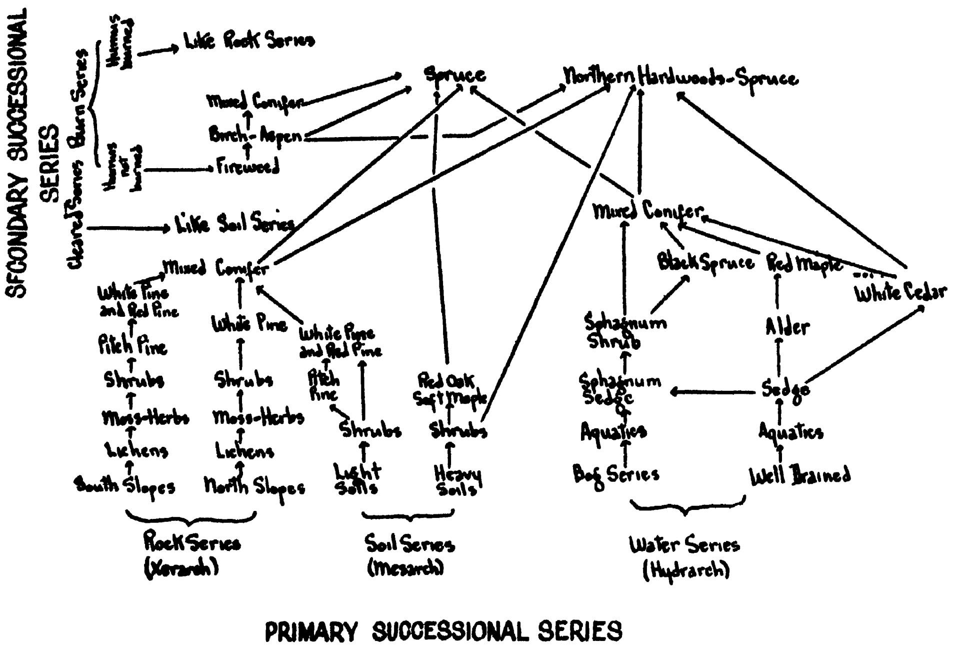

FIG. 14. Chart showing stages in the successional series in the development of the vegetation of Mount Desert Island

Two climatic climaxes are recognized by us as the ultimate destiny of the vegetation of the island, if left undisturbed. These are the spruce type, and the northern hardwoods-spruce type, both already briefly described.* The climax spruce type is not always composed of pure stands, but will have varying amounts of white pine, cedar and other species, the white pine forming a comparatively small percentage of the numbers, but rather substantial portion of the volume.

We have also recognized one and possibly two physiographic climaxes: the pitch pine on certain extreme sites, and perhaps also the white cedar.

* The fir type is also a true climatic climax, but not likely to occupy any more of the island than it now does, except possibly for its immediate surroundings on the summit of Cadillac (Green) Mountain. See page 29.

Pure stands of white cedar are restricted to sites which appear to have special soil and moisture conditions, but it is by no means certain that, as the swamps fill up, the spruce, or in certain places the northern hardwoods-spruce will not come in and crowd the cedar into a subordinate position.

There is a vast difference between the environmental conditions existing on the stark rock expanses and in the cool of the dark spruce woods. Instrumental data in another part of this paper show this contrast, and some of the conditions in the intermediate stages. But the vegetation itself is perhaps the best of all records, for here one finds the truest expression of what a habitat can, at the moment, produce. If the plant composition of these different habitats is rightly interpreted, it will show also to what vegetation types they are trending, or in some cases, will reveal the fact that, because of some local condition, vegetative development has reached its utmost limit. Such cases of obviously arrested development may often include what are apparently perfectly complete climaxes, but a study of the two climax forests of the island indicates that these local and unsuccessful attempts to reach the more complete goal are merely local examples of checked normal development of the vegetation.

Generally speaking, such cases of arrested development are rare, and we may see practically all stages, in numberless examples over the island, where now one and now another is temporarily dominant, but where the ultimate goal or climax is quite clear.

The most serious factor in disturbing the natural march of vegetative events is, of course, fire, which may in a day destroy ecologic conditions of almost incalculable antiquity. For the destruction of moisture-holding humus, its myriad microscopic inhabitants, and opening to a flood of sunshine a hitherto canopy-shaded forest floor, may completely alter or temporarily stop the normal succession. When it is recalled that fire sweeps with quite Olympian disregard of the vegetative destiny through any one of a half dozen different stages of succession, the complexity of its effects is obvious. Because of this we have placed considerable emphasis upon it in what follows, particularly in those cases where it has destroyed forest which had actually or very nearly reached the climax stage. Clear cutting may be destructive of natural habitats, but there is not the wholesale destruction of humus, which comes with a disastrous fire. Unfortunately in the past the limbs and tops have been left lying about, and cuttings have been followed by fires more frequently than not.

On soil, as distinguished from bare rock expanses, the incalculably slow process of rock destruction and soil formation has been unnecessary, and the development of vegetation has been more rapid. In describing the dif-

ferent vegetation types or associations the starting point in the developmental series, whether rock, soil, or water, will be used as the basis.

Rock Ledges and Talus Slopes

Whatever may have been the post-glacial history of the island, and whether or not the great areas now characterized by rock were once covered with plants, it is certainly true today that large stretches of country are either practically without vegetation or exhibit those first stages of succession which

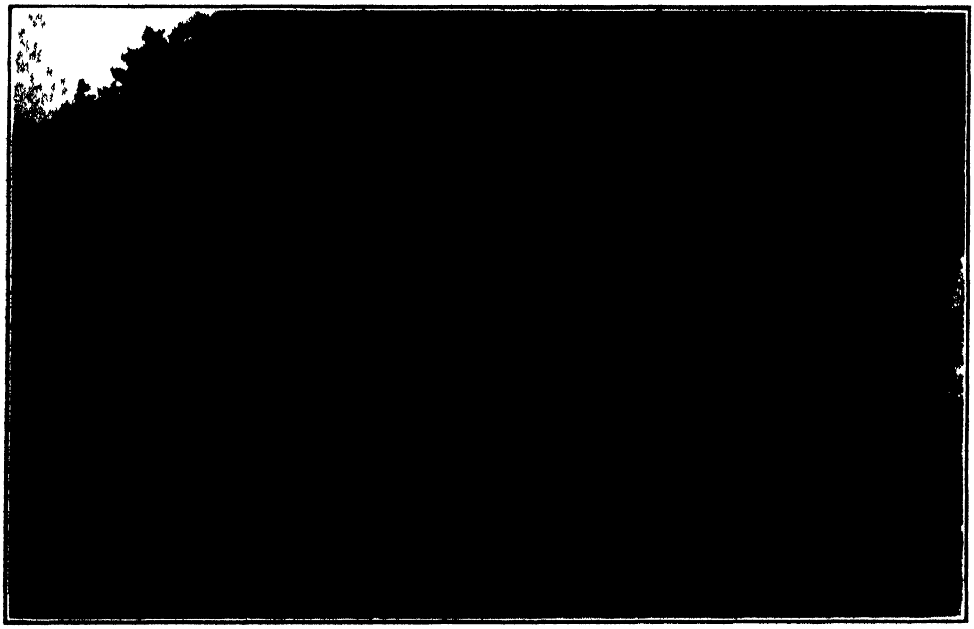

Fig. 15. Portion of a talus slope on west side of north ridge of Champlain (Newport) Mountain. Lichens on rocks, and colonization by white birch in the more favorable spots.

result in capturing the most unfavorable sites (see Fig. 16). That these rock expanses, except on northerly exposures, are unquestionably warmer than any other habitat is shown by the preponderance of plants of southern affiliations, which ultimately grow in such places. Details of this are presented elsewhere, but some isolated temperature records are inserted to show the differences between these south facing rock ledges and the rest of the region.

On Acadia (Robinson) Mountain on a south exposure (Fig. 18) an hour after noon on September 8, 1921, the bare rock registered 96° F. Under the thin sods made up of the roots and foliage of the bearberry (*Arcto-*

staphylos Uva-ursi) the temperature was 77° to 72°, depending upon the thickness of the bearberry, which here grows on bare rocks. The maximum shade temperature that day, as given by the U. S. Weather Bureau, for the Maine Coast was 65°. So that these bare rocks in the middle of the island were, and on most clear summer days are, 20° to 30° warmer than the air temperature. Much greater differences between the air and surface of the soil are not uncommon. Toumey and Neethling (1924) found differences of 60° F., and temperatures as high as 152° F. at the soil surface. Temperatures of 130° F. were fatal to coniferous seedlings.

The next day at Bennet Cove, which is close to the sea, the maximum air temperature was (for the coast of Maine) 63° F., while on the bare rock just under the roots of *Corema Conradii* the temperature was 77°, and the bare rock itself as warm as that on Acadia (Robinson) Mountain the day before. As has been shown above, the cool sea water, which even in midsummer does not reach a temperature of 55°, directly affects only a comparatively narrow coastal fringe, and, as at Bennet Cove and scores of other places, its cooling effect is lost if there are large rock expanses, the heating up of which counteracts the cool air from the sea.

Upon these rock expanses (Fig. 15) and upon gigantic talus slopes such as those on the sides of Cadillac (Green), Champlain (Newport), Huguenot Head (Pickett) and Penobscot Mountains, there are still large areas practically without vegetation except in the crevices. On the rock between the crevices and hollows there is no chance for the collection of water or accumulation of soil. The process of colonization must take place through the spread of creeping plants from the crevices and through the growth of drought resistant lichens on the open ledges (Fig. 16). The larger the proportion of crevices the more rapid the process. The rate at which the lichens form soil by the disintegration of the rock and the accumulation of rock particles and humus from their own remains is exceedingly slow.

Scores of different lichen species are known from the island (Plitt 1924), and in any discussion of the part these plants play in the first stages of succession, we must distinguish between those that actually help to manufacture or transform a site into something more favorable for later types of vegetation, and those lichen species which, like the earlier flowering plants outside of the crevices, are there because some pioneer work has already been done. In other words, it is to these actual pioneer lichens and to the spread of mat-forming plants from the crevices that we owe the appearance of later and more permanent types of vegetation.

The rock disintegrating forms are the crustose lichens which grow so firmly attached to the rocks that they can be collected only by chiselling off

the rock itself. Chief among these are *Rhizocarpon geographicum, Lecanora gibbosa,* and *Lecanora cinerea.* The foliose lichens are often more conspicuous and, while they are secondary to the crustose forms in breaking down the rock, play an important part in succession. The principal foliose species on the rocks of Mt. Desert Island are *Parmelia conspersa, Gyrophora deusta, Gyrophora Muhlenbergii,* and *Parmelia saxatilis.* After these come *Stereocaulon paschale* and the various Cladonias.

FIG. 16. Earliest stage in the development of vegetation on a granite ledge The two circular lichens are *Parmelia conspersa* (Ehrh.) Ach., beginning the process of forming humus and soil. Photograph reproduced by courtesy of E. T. Wherry.

The position of these rock inhabiting lichens, standing as they do upon the very threshold dividing the vegetatively impossible from the highly developed forests, is perhaps of more importance than many other plants which attract greater attention. For they are the actual pioneers which make ready the conditions that ultimately result in their own destruction. When later and shade producing types of vegetation are able to usurp the places that have been made by the lichens, the pioneers, as in most human societies, are inundated by more complex conditions.

The following is a list of the more conspicuous forms, *Gyrophora Muhlenbergii,* with its large masses, being easily the most prominent.*

* Collections of lichens were made in most of the plant societies of the island. These have been kindly determined for us by Mr. R. S. Williams of the New York

Rock Inhabiting Lichens of Mt. Desert Island

Gyrophora Muhlenbergii
Gyrophora deusta
Gyrophora Dillenii
Stereocaulon paschale
Parmelia physodes
Parmelia stygia
Parmelia saxatilis
Parmelia conspersa
Cladonia furcata
Cladonia caespiticia
Umbilicaria pennsylvanica
Umbilicaria pustulata
Rhizocarpon geographicum
Lecanora gibbosa

Some of these species are also occasionally found on soil, or among detritus, but all of them are found on rocks, and most of them nowhere else.

The slight accumulation of humus caused by most of these lichens is not enough to support flowering plants, nor can it lower the temperature enough, nor conserve enough rain water to permit the establishment of such inveterate inhabitants of rock ledges as the three-toothed cinquefoil (*Potentilla tridentata*), the chokeberry (*Pyrus melanocarpa*), the blueberry (*Vaccinium pennsylvanicum*), or the ground juniper (*Juniperus communis depressa*). For, beyond the necessary but wholly preliminary work of breaking down the rock, which even in the most favorable case is an almost incredibly slow process, there is the still more important one of covering as much of these bare rocks as possible. Other species of lichens and a few mosses appear to be almost the only plants that can get a foothold in such places. Some of them cover considerable areas and are, of course, of tremendous importance in changing the ecological conditions. Details of the process of building up rocky sites by pioneer lichen and moss associations may be found in Cowles, 1901, 1911, Cooper, 1913, Fink, 1903, and A. M. Taylor, 1920. One of the chief lichen genera to help in the accumulation of humus is *Cladonia*. Over many rock ledges there are solid sheets of *Cladonia rangiferina minor*, interrupted by the herbs and shrubs spreading out from the crevices, and associated with many other lichens and with mosses. Upon reaching this stage, the vegetation for the first time begins to be of use as a conserver of water. For these lichens and mosses that grow in mats, however thin, act as natural sponges, holding the rainfall for days, after the bare rocks have drained or dried it off. As we shall see presently the capacity to grow in dense mats, to accumulate humus and to conserve moisture makes these lichen-moss plant societies of the greatest importance.

Botanical Garden. The much more extended observations of Professor Charles C. Plitt, of the University of Maryland, part of which has been published in *Ecology* 5: 95–98, 1924, have materially increased the knowledge of the species of Mt. Desert Island. Professor Plitt, in correspondence with us, has also indicated the habitat of the different species. From his notes and our own the following list has been prepared.

Beside *Cladonia rangiferina minor*, another species, *C. gracilis elongata*, together with *Cetraria lacunosa*, which is often locally dominant, are important constituents of this lichen-moss association. While technically they grow on soil and make extensive mats, they are all found mostly on rock ledges, where the accumulation of soil has been sufficient to sustain them. The lichens mostly observed in such places by us or by Professor Plitt were the following:

Cladonia rangiferina minor
Cladonia gracilis elongata
Cladonia turgida
Cladonia pyxidata
Cladonia uncialis
Cladonia sylvatica
Cladonia furcata
Cladonia furcata pinnata
Cladonia alpestris
Cladonia squamosa
Cetraria lacunosa
Lecidea vernalis
Baeomyces roseus

With these are a few species of mosses which even more than the lichens help to conserve moisture, and by their own decay materially add to the humus content of the site. The moss genera which chiefly help in this are *Hedwigia* and *Grimmia,* both containing species that can stand a good deal of drying out.

Upon these mats of lichens and mosses there is the first appearance of flowering plants, except, of course, from those in the crevices. They do not always manage to survive, for unless there is considerable accumulation of humus, and the mat is more than a mere flat slab, a severe drought such as the 21-day period ending September 6, 1921, will leave hundreds of them dead or nearly so. It is a common sight also to see venturesome tree seedlings, which have prematurely established themselves in such a moss-lichen society, succumb to a drought which they might easily have survived if they had been growing in a greater depth of humus. There are so many hundreds of acres of Mt. Desert Island still clad in this grey-green mantle of lichens and mosses that it is a matter of practical importance as to which flowering plants really have the power to withstand conditions which are not quite impossible for drought resistant species, but wholly so for more moisture-loving plants. So often the accident of seed dispersal will temporarily populate these moss-lichen mats with plants whose withered remains, after a drought, are mute testimony of their unfitness for this still essentially pioneer plant association.

But certain flowering plants, by their habit of growth, texture of leaves and water requirements, are evidently fitted to withstand the conditions. Chief among these is certainly the three-toothed cinquefoil (*Potentilla tri-*

dentata), while the chokeberry (*Pyrus melanocarpa*) with fewer individuals is the almost invariable companion of the *Potentilla.* In scores of such places, on rock ledges or crevices, both these species are pretty nearly dominant. On the rock of the less exposed sites, and on the talus slopes, the common polypody fern (*Polypodium vulgare*) is generally the dominant plant in the lichen mat. This plant also grows in the sheltered crevices on south facing slopes. The pioneer herbs and low shrubs on the drier rocky sites, based on studies in many such places, are, in the usual order of their frequency:

Potentilla tridentata
Pyrus melanocarpa
Danthonia spicata
Vaccinium pennsylvanicum
Juniperus communis depressa
Kalmia angustifolia
Solidago Randii
Solidago bicolor
Arctostaphylos Uva-ursi
Pteris aquilina
Aspidium spinulosum intermedium
Aralia nudicaulis
Hudsonia ericoides (not on all sites)

While these plants are not, of course, the exclusive inhabitants of these rocky sites they are in great measure the pioneers, and the first four are found in practically every place of the kind on the island. They, more than any other flowering plants, seem best able to withstand the rigorous conditions of exposure, dryness and heat inevitably associated with such environments.

These herbs and low shrubs are not the only ones that play a part in the struggle to produce a substratum which will maintain a higher form of plant association than they can ever themselves become. Associated with them is a group of plants, not always found in all such places, but usually forming a considerable part of the vegetation. These secondary herbs and low shrubs, arranged in the order of their usual frequency, are the following:

Cornus canadensis
Trientalis americana
Maianthemum canadense
Aster acuminatus
Aralia hispida
Gaultheria procumbens
Aspidium spinulosum
Oryzopsis asperifolia
Melampyrum lineare
Deschampsia flexuosa
Solidago puberula
Panicum depauperatum
Prenanthes trifoliolata (stunted on these sites)
Aster umbellatus

It often happens that one or another of these primary or secondary herbs will become locally dominant in certain sites, and it is often true that certain

of them will be lacking. But the significant thing about them from an ecological point of view is not the lack or dominance of first this species or again of that, but the presence of one or all of them in sufficient quantity to make by their decomposition some material addition to the humus content of the site. Upon this conception the particular species working these changes do not matter so much, for the occurrence of any one of them must be largely due to chance or the result of vicissitudes of geographical distribution. Generally speaking, it is to these herbs and low shrubs that the appearance of higher woody plants is due, as the more permanent root systems of the latter demand greater depth of humus or soil: and humus, on these sun-smitten rocks, can come only from the pioneer work of first the lichen-moss carpet and then the herbs and low shrubs. Both the lichen stage and the colonization by woody vegetation are well shown in figure 3, page 38.

The Advent of Higher Woody Vegetation

The dominant woody plants to occupy the sites that have reached the stage of succession last described above are all low shrubs, some of them naturally so, others compelled by the poverty of the environment to assume such stunted forms. Shallow-rooted, as their substratum demands they must be, they are at the mercy of a prolonged drought.

But even stunted and intermittently withered shrubs are of immense significance in the scheme of succession from bare rocks or soil to forest growth, for they at once introduce to the site two factors of tremendous importance. The annual litter of their leaves gradually builds up the humus to depths and richness impossible before their arrival; and they begin, in a small way, compared to what is to follow, the shielding of at least some part of the site from the desiccating winds off the bare rocks. A few odd stunted shrubs, apparently scattered at random over the carpet of lichens, mosses and herbs, may not seem of much importance. By themselves, and without their potentialities being understood, they may not be. But over a period of years, and with the impetus to continue building up the environment unchecked by fire, this initial appearance of woody plants is of well nigh dramatic import. For, even the smallest of them, and perhaps because of their very stunting, produce annual crops of seed. In the case of certain dwarf blueberries, the crop is large enough to make the picking a worth while seasonal task for many women and children. The natural increase of these shrubs is checked only by the relatively limited environment open to them. As we have seen, the neighboring bare rocks are impossible; and, as most of them are light demanding species, the advent of a heavy forest canopy spells their doom.

Comparatively few shrubs are to be considered typical of the shrub stage in the successional series (see Fig. 3). The dominant species on the warmer sites are the low sweet blueberry (*Vaccinium pennsylvanicum angustifolium*, or sometimes merely *V. pennsylvanicum*), the black huckleberry (*Gaylussacia baccata*), the black chokeberry (*Pyrus melanocarpa*), the ground juniper (*Juniperus communis depressa*), or the sweet fern (*Myrica asplenifolia*). On the cooler sites the blueberry is still very abundant, but has more and different associates. Perhaps the commonest are the sheep laurel (*Kalmia angustifolia*), the downy green alder (*Alnus mollis*), and the bush honeysuckle (*Diervilla Lonicera*).

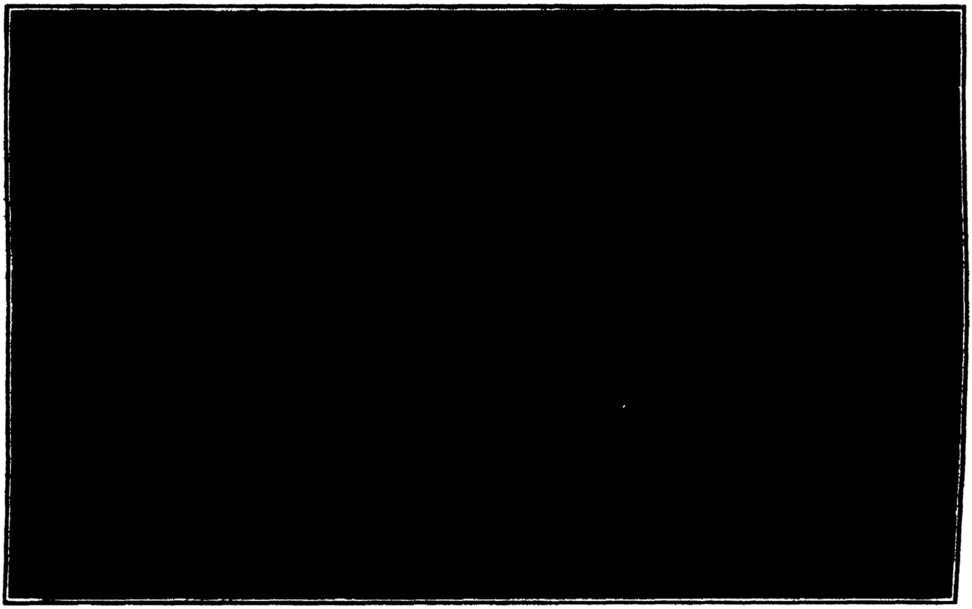

FIG. 17. Shrub stage at Bennet Cove. Dense mat of broom crowberry (*Corema Conradii*) in left foreground. Shrubs are bayberry (*Myrica carolinensis*), sheep laurel (*Kalmia angustifolia*), black chokeberry (*Pyrus melanocarpa*) and huckleberry (*Gaylussacia baccata*). The tree seedling in the center is red pine (*Pinus resinosa*).

Almost as frequent, but nowhere so dominant as these shrubs, are others which, like their more ubiquitous and plentiful associates, are also dwarfed since they are found in these still inhospitable rocky ledges. One of them, the mountain holly (*Nemopanthus mucronata*), is remarkable for the stunted, small-leaved and pinched aspect it takes on in such places as compared to its much better development in more favorable spots over the island.

At some places, notably at Bennet Cove (Fig. 17) and in the region around Bass Harbor, the broom crowberry (*Corema Conradii*) usurps the

position of, but does not entirely exclude, the foregoing. Here the ground is literally carpeted with this usually rare shrub. Again there are places where the downy green alder (*Alnus mollis*) will be locally dominant, such as it is wholly over many square rods near the top of Acadia (Robinson) Mountain, and partly on the bleak summit of Canada Cliffs. Including those already mentioned, the shrubs observed on these lichen and moss-covered rocks are, arranged in their usual order of frequency, the following:

Vaccinium pennsylvanicum
Vaccinium pennsylvanicum angustifolium
Gaylussacia baccata
Pyrus melanocarpa
Myrica asplenifolia
Nemopanthus mucronata
Kalmia angustifolia
Alnus mollis
Myrica carolinensis
Diervilla Lonicera
Corema Conradii

It may well seem as if this were a meagre list of shrubs to cover so much ground. As a matter of fact many other species are found among these pioneer woody inhabitants of rocky places. But the dominance of those listed puts them in a separate category on such sites. While the beautiful Rhodora (*Rhododendron canadense*) for instance is often found mixed with these shrubs, its natural home, judging by its much finer development in other parts of its range, is not on rocky windswept ledges. The same is true of the withe-rod (*Viburnum cassinoides*), which is locally very common and sometimes almost subdominant in such sites. That it tolerates places like this rather than seeks them is evident enough to those who know it in its finest development among its usual associates of moist sites.

Any one of the total shrubby species of the flora of the island, with a few bog exceptions, is likely to be found with the dominant species. Many such have been. But to list them as being in any true sense significant in the general succession of vegetation is to drag them from their proper niche in another part of that scheme, and put them in a place where their occurrence appears to be an accident and is certainly in most cases an ecological futility. While telescoping of plant associations does occur on the island, as we have already pointed out, the sporadic occurrence of plants from moister environments in these exposed and still essentially dry associations is not an example of it. Much more likely is it that these interlopers from possibly adjacent forest, or swamp, or bog, have found occasional moist spots in crevices or rocky hollows of the surrounding dry site. We have put, perhaps, more stress upon this than it is worth, because it is so common all over the island, not only with the shrubs, but also in the case of tree seedlings, as will appear

later. But it is obvious that there is much difference between the shrubs listed above and these others that play only a small and often temporary part in it; and that there are vastly greater potentialities in the shrubs that by their frequency, dominance, habits, and generally xerophytic adaptations are quite obviously making a direct and effective contribution toward building up the succession.

This march of vegetative events on these rocky places is not always characterized by such an orderly procedure as the above account might imply. In a region like Mt. Desert Island, with a rainfall such as our figures elsewhere have shown, the tendency, we might almost call it the urge, to produce a forest is very strong. It is to this fact that we owe the appearance of trees wherever, on rocky ledges or talus slopes, there is the slightest chance of their survival. And in all such places there are, of course, crevices or even clefts in the rock, or upon talus slopes some fortuitous mixing of the boulders, that allows deeper accumulations of humus than is usual. In many of these there are usually found small trees, white birch, cedar and spruce most frequently, which tend to make the transformation of the site more rapid than it could otherwise be. Even an occasional small tree, by its shade and the accumulation of fallen leaves, makes growth conditions much more favorable than the sort of vegetation we have just described.

On bare rocks over which salt spray is dashed during storms, and which are kept much cooler by their proximity to the sea water, the plants are very different from those already mentioned. Among the commonest species in such places are *Campanula rotundifolia*, *Juncus Greenei*, *Agrostis hyemalis*, *Plantago decipiens*, and often *Ligusticum Scothicum*. *Prenanthes nana* and *Solidago Randii* are often scattered through these herbs, but the most conspicuous plant is the crowberry (*Empetrum nigrum*) which often covers square rods of these rock cliff edges. Except in certain bogs the crowberry is more common along the shore cliffs than anywhere else on the island.

PIONEER PLANT ASSOCIATIONS ON SOIL

While the capture of rocky ledges and talus slopes is, as we have seen, a slow and often interrupted process, there is a much quicker and more direct method for the vegetation to capture other parts of the island that are already provided with soil. The richness and moisture-holding capacity of these soils from different parts of the island may vary one from another, but they all agree in being very much more favorable for plant growth than the thin poor soils that characterize the sites just described. With greater depth, and with a good deal better chance to hold accumulated humus, these places are of importance because it is upon them that forest growth is most satisfactory.

It is the time required for the establishment of a forest cover that distinguishes these sites possessing soil from the rock ledge or talus plant associations. Superficially, and often actually in the earlier stages, there is little difference between the plant societies that grow in the two places. Both are open, both still subject to high evaporation, and the general similarity of their aspects and even of the species and frequency of them is remarkable. But upon those that are underlaid by soil of any reasonable depth there is ultimately a greater profusion of shrubs, and those tree seedlings that do gain entrance are much more likely to survive and grow at a reasonable rate.

Perhaps the chief characteristic of such places is that, unlike the rock ledges or talus slopes, they provide, in a sense, a ready-made substratum. What in the one case is an almost incredibly slow process, subject to any number of interruptions and sometimes halted in mid-career, is in the other a *fait accompli*. Upon that fact alone depend the forest potentialities and much greater number of species which grow in such places. In the march from dry to moist conditions, the vegetation of the island naturally becomes sorted out into different categories; and in the case of the sites under discussion, we find for the first time a list of species that are never found, or if so only sporadically and probably ineffectually, in the rocky places. This new group of decidedly more moisture-requiring herbs and shrubs is often mixed with, and in some places even temporarily dominated by, the herbs of the rocky places. But, generally speaking, the number of species and profusion of those which demand more moisture is a striking characteristic of these sites.

The area covered by soil is, of course, much greater than by rocks so that the plant associations inhabiting soil are much more extensive. To describe them in detail would lead to a discussion of the better part of the flora of the island, with all the variations which slope, available moisture, and forest canopy would dictate.

A typical piece of this vegetation is to be found in the more open parts of the mixed conifer forest at Hulls Cove, and a description of this will give as good a picture of this stage of succession as the situation affords. The place is a medium dry site. The canopy is made up of red spruce 40.9 per cent, white pine 28.6, cedar 5.5, red pine 2.4, fir 0.6, red maple 10.9, white birch 5.5, red oak 4.2, and aspen 1.2. The characteristic herbs of the open are the wild sarsaparilla (*Aralia nudicaulis*), and the bracken (*Pteris aquilina*), which together make up eighty-five per cent of all herbaceous vegetation. The balance of the plants, arranged in order of frequency, are the following:

Maianthemum canadense Gaultheria procumbens Cornus canadensis Linnaea borealis Trientalis americana	about 5 per cent of total herbs
Clintonia borealis Chimaphila umbellata Pyrola americana Polypodium vulgare Chiogenes hispidula Viola septentrionalis Lycopodium tristachyum Oryzopsis asperifolia Melampyrum lineare Aralia hispida Aspidium spinulosum	about 10 per cent of total herbs

From this list of herbs it will be seen that, while there is an appreciable amount of soil and of humus, the place, at least so far as the openings are concerned, is still rather dry. For eighty-five per cent of all the herbs are species that by their dominance on rocky sites prove their fitness for such places. And in the list of species that total only fifteen per cent of the herbs, at least some are to be considered as on the drought-resistant rather than on the moisture-requiring side.

There are among these herbs characteristic shrubby growths and scattered patches of lichens where local intrusions of rock make only these possible at present. It is in this that the significant difference of the place from the rock ledges and talus slopes speaks most eloquently. All the shrubs are taller, better furnished with foliage, and in their every aspect show reaction to the more favorable site. The characteristic shrubs of such places are, in their usual order of frequency, the following:

Gaylussacia baccata	Rubus hispidus
Alnus mollis	Rubus canadensis
Viburnum cassinoides	Myrica asplenifolia
Nemopanthus mucronata	Vaccinium pennsylvanicum
Diervilla Lonicera	Vaccinium Vitis-Idaea
Kalmia angustifolia	Pyrus melanocarpa

While it is still true that comparatively drought-resistant shrubs head the list, and consequently make up the bulk of the shrubby vegetation, at least

some of the others indicate that a site like this with some depth of soil is far in advance of anything hitherto considered. It is of interest, as showing what these herbs and shrubs signify to record the tree seedlings which are already making a bid for occupancy; not only making a bid, but, aside from the fir, rather sure to capture the site in the end, as the thriftiness of the seedlings only too surely testifies. The tree seedlings observed, with the percentages of each species, are:

Species	Per Cent
Fir	54.4
Spruce	26.7
White Cedar	11.1
White Pine	7.8

These figures do not, of course, show the composition of the mature forest, for, as we shall show presently, a great deal happens before that consummation is reached. The list is inserted here as an obvious indicator of what such on open place, possessing soil, will produce, and as a contrast with the much slower example of the same process, as we have observed it, in the rocky places where the accumulation of soil is still too scanty.

THE PITCH PINE

To anyone familiar with pitch pine on Long Island or New Jersey, the Mt. Desert Island specimens seem poor, stunted and lacking in canopy-density (see Fig. 4). While these specimens are not at the northern and eastern extremity of the range of the species, they are so far away from the region where it makes its best growth that it is little wonder they look anything but thrifty.

Whether or not the pitch pine is actually a stage in the development of the vegetation of the island, or whether it is merely a drought-resistant forest type that is permanently inhibited from further development, does not lessen our interest in this pine, which is *the* tree of the pine barrens of Long Island and New Jersey, and appears far out of its element on this predominantly spruce clad island.

Evaporation and soil temperatures are higher in the pitch pine than in any other forest type on the island. Not only was this type the highest of the four stations described above on pages 62–68, but our figures, somewhat fragmentary but consistent, show that in dryness it even exceeds the scrub oak site on Acadia (Robinson) Mountain (see below, pp. 106–109). Wherever, due to exposure, slope or vegetative covering, the heat of the bare rocks is masked and evaporation lowered, the general cool climate of the island is

sufficient to keep out the pitch pine. That is why it is invariably found on rock ledges, or rocky summits like Kebo and Huguenot Head (Pickett), never, as a forest type, on north exposures. There are scattered pitch pines almost throughout the island, where local exposure of rock will permit.

While the origin of this tree on the island may be obscure, and our suggestion of its method of arrival in earlier pages of this account may not be the true one, its confinement to the dryest and warmest sites is noteworthy. It is as if, forest vegetation being obligatory, but the climatic climaxes of spruce or northern hardwoods-spruce being impossible, the best expression of forest growth that *can* mature in these warm rocky places is the pitch pine.

The forest itself, aside from the under vegetation, has already been described in connection with the general characteristics of the forests of the island (see p. 31) and also under the account of the forest at the four instrumental stations (pages 37–40).

Under this rather thin canopy, which nevertheless distinctly ameliorates the conditions that obtain in the rocky places described earlier, the shrubs and herbs are still overwhelmingly of the drought-resistant type. Practically all the shrubs already noted are found under, or it is perhaps more correct to say, among, the pitch pines, at nearly every place that the tree has captured. At Huguenot Head (Pickett Mountain) ninety-five per cent of the shrubby vegetation is made up, in the order of frequency, by the huckleberry (*Gaylussaccia baccata*) the sheep laurel (*Kalmia angustifolia*), the black chokeberry (*Pyrus melanocarpa*), the withe-rod (*Viburnum cassinoides*), sweet fern (*Myrica asplenifolia*), and the mountain holly (*Nemopanthus mucronata*). In some places, where even these cannot get a foothold, there are large exclusive patches of the prostrate juniper (*Juniperus communis depressa*), or the low blueberry (*Vaccinium pennsylvanicum angustifolium*) and the bearberry (*Arctostaphylos Uva-ursi*).

Local variation exists as to the shrubby species associated with the pitch pine, the reasons for which are not always clear. While we have instrumental data from the pitch pine only on Huguenot Head (Pickett Mountain), it may safely be assumed that other places on the island where this pine has become established must be somewhat similar ecologically. But at Bennet Cove, Rhodora (*Rhododendron canadense*), and the broom crowberry (*Corema Conradii*), in addition to the shrubs already mentioned, make up a large proportion of the woody vegetation of the ground cover, probably accounted for by the more favorable conditions due to proximity to the sea. At Bear Brook hill, which has a lower evaporation than Huguenot Head (Pickett), practically the only shrub among the pitch pine is *Viburnum cassinoides*. At the summit of Kebo, where conditions are similar to those on

Huguenot Head (Pickett), only less severe, the pine's shrubby associates are much the same as at Huguenot Head (Pickett), with the addition of *Diervilla Lonicera*. As we have already pointed out, there are also occasional intruders from whatever forest type may happen to surround the pitch pine, but the discovery or recording of such is scarcely significant from the point of view of the development of the vegetation.

It is among the herbs that we find the most interesting group of species in the pitch pine forest. The total flora of the island is made up, generally speaking, of plants that are never associated with this pine in the more southern part of its range, for they do not get down on the coastal plain anywhere near the vicinity of New York. At the same time, and often mixed with these northern herbs, are such characteristic associates of the pine as the pink ladies' slipper and prince's pine. The apparent ecologic incongruity of these herbs growing closely associated with the twin flower (*Linnaea borealis*), and the little creeping snowberry (*Chiogenes hispidula*), is one of the first things to strike one about the pitch pine groves. For here are two groups of herbs—we have mentioned only these two to illustrate the point, but there are others—one decidedly from the north, the other much more common on the warm sandy coastal plains of Long Island and New Jersey. In a small way, they point to the chief fact of interest about the vegetation of Mt. Desert Island. Scarcely anywhere else along the coast could one find, in such quantity, a meeting ground of vegetation types of such diverse origin as on this island. And because the pitch pine and scrub oak growths furnish almost the only chance for the survival of the species that have come with them from the south, while still affording conditions not impossible for the decidedly northern herbs that make up the bulk of the flora of the island, these growths are of outstanding interest. As we shall see later, the herbs generally associated with the more highly developed forest types are, with minor and unimportant exceptions, what are to be expected in such forests and could be duplicated in the same forest types over thousands of acres of the Catskills, Adirondacks, or the upland parts of New England. It is only in the pitch pine and scrub oak localities that we find best developed the mingling of northern and southern plants.

A list of herbs and low shrubs that have been found in different pitch pine groves on the island, in addition to those mentioned above, with some notes on their usual frequency, is presented here as a record of how complete has been this mingling. Not all of them are found at every occurrence of the pine, nor do some of them always grow with the frequency indicated by their position in the list. But, generally speaking, these are the herbs and low shrubs of this forest type.

Potentilla tridentata, nearly always dominant
Pteris aquilina, very common
Aralia nudicaulis, dominant in group of pitch pine on Bear Brook Hill
Danthonia spicata, especially common at Huguenot Head (Pickett Mountain)
Aralia hispida
Corema Conradii, known only from Bennet Cove, under the pitch pine, but at many other places on the island
Hudsonia ericoides, very common at Bennet Cove
Solidago Randii, the commonest goldenrod at Huguenot Head (Pickett Mountain)

These seven are the most frequent plants. In some groves of the pine, notably that at Bennet Cove, *Corema Conradii* is dominant. The secondary species are:

Melampyrum lineare, rather rare except at Bennet Cove
Panicum depauperatum, rare, only seen at Kebo
Polypodium vulgare
Euphrasia canadensis, only seen once from Bennet Cove
Trientalis americana
Arenaria groenlandica, rather common on Huguenot Head (Pickett Mountain) and elsewhere in openings on the rock among the pitch pine
Aster umbellatus
Gaultheria procumbens
Cypripedium acaule
Deschampsia flexuosa, common at all stations
Solidago bicolor
Chimaphila umbellata, uncommon
Maianthemum canadense, rather common at Kebo and Bennet Cove
Aspidium spinulosum intermedium
Solidago puberula
Cornus canadensis, often locally dominant
Aster nobilis,* often locally dominant
Viola blanda, rare, in a group of pitch pine on Bear Brook Hill

A reference to the herbs which characterize rock ledges and talus slopes shows how much the occurrence of the pitch pine has added to the opportunity

* Not maintained in Gray's Manual but kindly identified for us by Dr. Edward S. Burgess.

for a more varied list of herbs to become established. While there is still, in the pitch pine a large proportion of the herbs that dominate rock ledges and talus slopes, it is evident that there are many more that are never found there, and we must credit even the meagre canopy of the pine with having made the advent of these new herbs possible.

It is obvious from the foregoing that the pitch pine has made some contribution to the number and frequency of the herbs that can grow in such places. What it does in the way of providing a place suitable for tree seedlings is another matter. It is, of course, upon the kinds and frequency of the latter that hope for the development of better types of forest depends. Either tree seedlings of more moisture-loving types will gradually, if they mature, spell the doom of the light-demanding pine, or else the still warm and dry site will so favor the reproduction of the pine and so hinder that of other trees as to enable the pine to maintain itself as an arrested climax.

Scrub Oak on Acadia (Robinson) Mountain

The growth of scrub oak (*Quercus ilicifolia*) on Acadia (Robinson) Mountain is one of the most interesting features of the vegetation of Mt. Desert Island (Figs. 18 and 19). So far as known at present it is found only on Acadia (Robinson) Mountain, although Rand and Redfield, in 1894, reported it from the adjacent St. Sauveur (Dog) Mountain. Diligent search for it on the latter failed to discover a single plant, while on Acadia (Robinson) it is common. Facing Echo (Denning) Lake (Fig. 19) the shrub comes down to the 225-foot contour and is scattered all the way up to the top. It is very plentiful on the southwestern and southern face of the hill, diminishing as one goes down toward Somes Sound, 25–50 feet above which the last stragglers disappear. No specimens could be discovered on the north slope of the hill.

Perhaps no other plant is so apparently out of key with its environment as this scrub oak on Acadia (Robinson) Mountain. Mt. Desert is, after all, an evergreen clad island, and, while much destruction of its former fine forests has gone on, there is the best of evidence that evergreens will eventually capture the island again. And yet, in the center of this overwhelmingly evergreen island is this great hill, the top and three sides of which are clothed predominantly by a scrub oak thicket such as covers thousands of acres on the hot sandy plains of Long Island and New Jersey.

It is not by any means sure that the scrub oak is a case of arrested climax. Although it is associated with pitch pine, it is doubtful if it can be considered the forerunner of this pine. A more probable view is that it is associated

FIG. 18. Precipitous south face of Acadia (Robinson) Mountain, showing the site on which scrub oak (*Quercus ilicifolia*) grows. Patch of this oak in foreground, and many other patches in the picture. View looking east, Somes Sound in right background.

FIG. 19. Scrub oak (*Quercus ilicifolia*) on a ledge of grey granite, southwest exposure, on Acadia (Robinson) Mountain at 225 feet elevation. Echo (Denning) Lake in the background.

with pitch pine under a special set of conditions found only on Acadia (Robinson) Mountain.

TABLE XIV. *Evaporation, Air Temperature and Relative Humidity in opening in Scrub Oak Association on Acadia (Robinson) Mountain, and opening in Pitch Pine Forest on Huguenot Head (Pickett Mountain), July 9, 1923*

	Evaporation in c c						Air Temperature in Shade		Relative Humidity %	
	Scrub Oak Acadia (Robinson)			Pitch Pine Huguenot Head (Pickett)			Acadia (Robinson)	Huguenot Head (Pickett)	Acadia (Robinson)	Huguenot Head (Pickett)
	White	Black	Solar Radiation	White	Black	Solar Radiation				
7 A.M.	.6	1.	.4	1.5*	1.2	—	67.5	66.5	71	60
8 A.M	1.3	2.1	.8	1.7	2.1	.4	72.5	70	67	58
9 A.M.	2.	2.8	.8	2.9	3.6	.7	76.5	71	63	56
10 A.M.	2.4	3.7	1.3	3.7	4.2	.5	83.	74.5	52	56.5
11 A.M	3.9	5.4	1.5	4.4	4.8	.4	86.5	82	47	56
12 M.	3.9	5.3	1.4	4.7	5.6	.9	86.5	85	55	41
1 P.M	4.5	6.2	1.7	5.4	6.1	.7	86.5	90	36	36
2 P.M.	5.3	5.6	.3	6.6	7.6	1.0	82.	86	48	44
3 P.M	5.3	5.6	.3	7.5	8.2	.7	80.5	80	46	45.5
4 P.M.	5.1	5.7	.6	7.0	7.5	.5	77.	77	59.5	47.5
5 P.M.	5.	5.3	.3	6.8	7.4	.6	75.	75.5	44	46
6 P.M.	4.2	4.7	.5	6.2	6.5	.3	73.	72.5	42	44
7 P.M.	3.5	3.6	.1	6.0	5.4	—	72.5	72	42	39
	47.0	56.8	10.0	64.4	70.2	6.7				

* Raised to per hour basis, actual corrected value was .9 for white. Black estimated, the instrument not working and changed for next reading.

In any case it is desirable to make some comparison between the sites on which the pine and scrub oak grow. In both, the conditions are probably more unfavorable for any forest of the climax type than any other places on the island sustaining woody growth at all. While evaporation, temperature and relative humidity are known to be decidedly unfavorable at both places, as shown by the general records for the pitch pine station on Huguenot Head (Pickett Mountain), given elsewhere in this paper, we were not certain that there was enough difference between the two sites to be ecologically significant. To test this we made synchronous hourly comparisons between two open stations, on Acadia (Robinson) and Huguenot Head (Pickett Mountain), from seven in the morning until seven in the evening of July 9, 1923. Atmometers

were set out in as nearly comparable sites as possible, the pitch pine station on Huguenot Head (Pickett) being our regular open station for atmometers during three seasons' work. The station on Acadia (Robinson) was about 75 feet below the summit, facing due south, and completely exposed to the southwest wind, except as this is intercepted by St. Sauveur (Dog) Mountain, which is about the same height as Acadia (Robinson) Mountain and whose summit is just a mile south, about 20 degrees west, of our station.

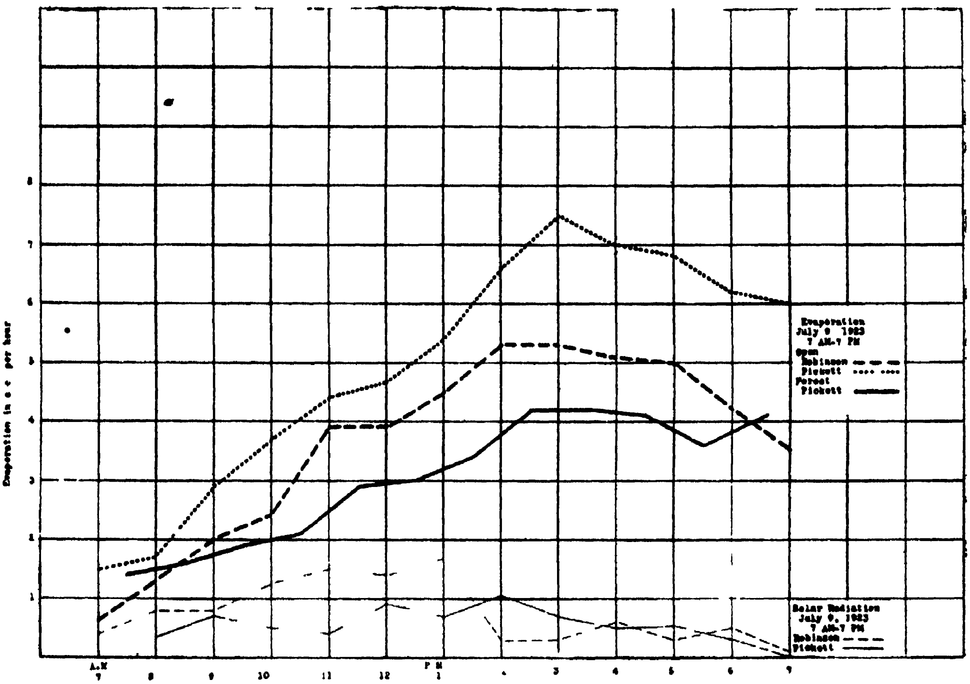

FIG. 20. Graph showing comparison between the course of evaporation for openings in pitch pine, Huguenot Head (Pickett), and scrub oak, Acadia (Robinson), for a single day. Evaporation in the pitch pine forest (heavy solid line) is also shown. The lighter lines at the bottom give the course of the solar radiation (difference between the Livingston black and white atmometers).

The result of this comparison, which is presented in Table XIV and figure 20, shows that the pitch pine forest on Huguenot Head (Pickett Mountain) is even more unfavorable than the scrub oak site. Temperature readings at both places were taken out in the open, the bulb about one foot above the surface, but the thermometers under a temporary wooden shade, which kept the instruments out of the sun, but not, of course, out of the influence of the heated rock and lichen-moss mats about them.

With the scrub oak evaporation from the white atmometer totalling 47.0

c.c., the pitch pine instrument lost 64.4 c.c. of water during the same period. For the black instruments the total was for the scrub oak 56.8 c.c. and for the pitch pine 70.2 c.c. Both of these are very high rates for a single period of twelve hours, but the weather was warm, nearly cloudless, and only became "smoky" with the freshening of the wind in the afternoon.

As has been stated above, the atmometers, particularly the black ones, are rather sensitive to violent winds. Black and white atmometers set out on the open downs at Montauk, Long Island (see Taylor, N., 1923), invariably evaporated more water during periods of high than during mild winds, in spite of decreased sunshine, and in certain cases of much reduced temperature. This experience is to a certain extent confirmed in the comparison between the scrub oak and pitch pine stations on Mt. Desert Island, where, however, the relative humidity played an important part, as the figures show. The evaporation at both stations stayed fairly low until ten or eleven o'clock, in spite of constantly mounting temperature and an absolutely cloudless sky. It reached its peak at 3 P.M. when the relative humidity reached its minimum, in the face of a falling temperature, and a sky that, while cloudless, was decidedly "smoky." Evaporation held near the maximum until the 5 P.M. reading when the temperature had dropped from ten to fifteen degrees from its mid-day maximum, and the sky was not only "smoky," but a few clouds were flying across, and plunging both sets of instruments under temporary shade. But the wind, which began about noon with light airs from the sea, had by five reached the force of half a gale and the humidity remained low. It is perhaps of more than passing interest that the *form* of the graph of evaporation under the pitch pine canopy resembled the *form* of the graph for the opening surrounded by scrub oak more closely than it did the open pitch pine station near-by. Thus it may be that the light pitch pine canopy mitigates extreme conditions sufficiently to bring the march of evaporation into close relationship with a more or less uniform trend which seems to prevail over at least a large part of the island.

As a check against this single day's comparison the atmometers were left in both sites for the week July 9–15, when the readings showed the following:

Rate per Day in C.C. of Evaporation at Huguenot Head (Pickett) and Acadia (Robinson) Mountains. July 9–15, 1923

Scrub Oak Acadia (Robinson) Mountain			Pitch Pine Huguenot Head (Pickett Mountain)		
White	Black	Solar Radiation	White	Black	Solar Radiation
38.1	45.4	7.3	59.2	64.3	5.1

This rate per day over the week confirms the single day's comparison of the two sites—the pitch pine is decidedly the drier.

A further check was secured in 1924 by means of Bates evaporimeters exposed on these two sites for two periods. The results were as follows:

EVAPORATION IN C.C. PER DAY FROM BATES EVAPORIMETERS FOR SCRUB OAK AND PITCH PINE, 1924

	Scrub Oak	Pitch Pine
June 9 to 27 (18 days)	7.9	8.5
June 27 to Aug. 1 (36 days)	8.61	9.23

It will be recalled that the Bates evaporimeters with blackened tops record insolation as well as evaporation. Since the higher insolation of the scrub oak compensates to a certain extent for its lower rate of evaporation, the Bates readings for 1924 agree with the records of the Livingston atmometers in 1923.

Unquestionably this dryness and insolation make Acadia (Robinson) Mountain a suitable site for the scrub oak. But there are other places on the island where topography, distance from the sea, heat and evaporation seem to be as good for the plant as on this particular hill. The only difference, which may or may not be of significance, is the fact that the parts of Acadia (Robinson) Mountain on which scrub oak grows are completely cut off from the sea by other mountains. All the winds which strike it must first pass over elevations equal in height to Acadia (Robinson) or higher. The pitch pine forest on Kebo is also cut off from the sea, but does not have the large expanse of rock cliffs. Nevertheless the isolation here of the scrub oak must always be something of a mystery.

Because of the interest attached to this large growth of scrub oak so far north and east of its center of greatest frequency, it has seemed to us worth while to put on record its manner of growth and its associates.

Over a good part of the hill there are rock ledges covered by the vegetation that has already been described as typical of such places. As a local variation of such plant covering we find a greater frequency of the grass *Danthonia spicata*, and a great luxuriance of the bearberry (*Arctostaphylos Uva-ursi*) which fruits more plentifully here than anywhere else within our observation.

On this rocky lichen herb-strewn summit there are the shrubs already listed, the local dominant being easily *Vaccinium pennsylvanicum angustifolium*, with an abundance of the low prostrate juniper (*Juniperus communis depressa*). None of these is over six inches high, as they are developed on the comparatively sterile summit, and it is among such a growth that the scrub

oak has become established. Wherever there is a little soil the oak is *the* dominant woody plant. Most of the specimens are not over six or eight feet high, some much less than this, but in a few cases, and in the protection of clefts in the rock, specimens up to ten or twelve feet are not uncommon. In nearly all places its close scrubby growth is so dense and unyielding that it is difficult to force one's way through the inextricably tangled branches. While the usual rate of growth of *Quercus ilicifolia* is not certainly known, it appears on Acadia (Robinson) Mountain as if it were rather slow. Ten specimens, picked at random, showed the following ages and diameters.

	Diameter Inside Bark in mm.	Annual Rings	Rate in mm. per Year
	21	9	2.3
	43	43	1.0
	29	23	1.2
	23	25	0.9
	38	31	1.2
	26	15	1.7
	18	20	0.9
	35	21	1.6
	19	14	1.3
	27	22	1.2
Average	28	22	1.3

The average rate of only 1.3 mm. per year (or about 20 years to grow an inch in diameter), may well be taken as a fair sample of the rate of growth for the scrub oak at this place.

While this small tree is easily the dominant woody plant over that part of the mountain it has captured, there are some indications that it may not have always grown here, and that ultimately it may be crowded out. It is decidedly light-demanding, so that under any other than the comparatively open-canopied pitch pine it would succumb. There is a fair sprinkling of rather dwarfed and stunted pitch pines scattered all over the area occupied by the oak. In addition to this, and of much more significance from the point of view of the survival of the oak are the seedling trees of red pine, quaking aspen, white birch, fir, cedar, spruce, white pine, and a few red oaks. As yet none of these occurs in sufficient quantity or size to be a menace to the scrub oak, but if, as seems difficult to imagine on this extraordinarily rocky mountain, they should ever reach forest proportions, the scrub oak would be either crowded . the most exposed and inhospitable ledges or be completely routed.

There is, too, some indication that the hill once sustained forest growth of some sort, since we found, sometimes half hidden by the scrub oak and

sometimes quite out in the open, the stumps of trees with diameters of a foot or slightly more. It is more than probable that these once formed a stand sufficiently open to permit the existence of the scrub oak.

SUMMARY OF PITCH PINE

Although there may be some doubt as to whether or not the pitch pine and its associated scrub oak on Acadia (Robinson) Mountain is to be considered an arrested climax, there is abundant evidence that most of the other stands of pitch pine represent merely a stage in the successional series. The case of Huguenot Head (Pickett) has already been fully discussed, and the reasons for considering it a physiographic climax have been explained. Under most other stands of pitch pine we find reproduction of white pine, fir, spruce and cedar which plainly indicate the trend of development.

Almost without exception, the open rock ledges that face south or southwest are at some stage in their history covered by a rather stunted pitch pine forest. Eventually this forest is invaded by other coniferous trees, most often the white pine or the red. As the pioneer forest type the pine ultimately gives way to a mixture of coniferous trees that is very widespread on the island. We have called it "mixed conifer" for want of a better term. Its composition has already been briefly touched upon (see p. 30) and will be more fully discussed below.

In the development of the vegetation of the island, the steps appear to be from the lichen-moss mat to pitch pine, and thence through white pine to the mixed conifer. It is evident from the instrumental records that the white pine forest is less drought resistant than the pitch pine, but more so than the mixture of pines and spruces which we call the mixed conifer type. While white pine is always a fairly large constituent of the mixed conifer, particularly on the drier sites, it was also found by the early settlers, towering as giant individuals, over the canopy of the spruce climax. Occasional trees still do. But as a forest type today it occupies only very little of the island.

WHITE PINE

The composition of the main canopy of the white pine forest has already been given on page 30, and a representative example presented in the description of the white pine instrumental station on pages 40–41 (Fig. 5), which is fairly representative of this type. We now come to the under vegetation, or forest floor, and the developmental trend of the type.

Wherever the white pine makes a closed canopy, it may almost be said that the forest floor is completely bare of under vegetation, aside from fir reproduction. There are square rods of the pine grove at Bear Brook Hill where there is hardly anything except a carpet of pine-needles, which are

nearly as acid as the duff under the spruce forest. Here practically no shrubs are found, and only a handful of herbs. The shade is too heavy, and the humus is rather dry owing to the constant drain on the moisture by the numerous roots of trees, to the run-off from the thatch-like mat of needles, and to the interception of precipitation by the tree crowns. Wherever an opening occurs there is at once a very different vegetative covering.

Nevertheless, even under the densest canopy some herbs do get a foothold, and these should be listed before we consider those with a better chance in more open conditions. At Bear Brook Hill, we found on the otherwise needle-strewn ground that the wild sarsaparilla (*Aralia nudicaulis*) was easily the best fitted, judged by its frequency, to become established under the densest part of the canopy. Beside this there were stray plants of the bracken (*Pteris aquilina*), the wintergreen (*Gaultheria procumbens*), the bunchberry (*Cornus canadensis*), and the twin flower (*Linnaea borealis*). A few specimens of a sedge (*Carex rugosperma*) were also found. But the poverty of herbs and the complete lack of shrubs under the densest part of this canopy is noteworthy.

At Fawn Pond, where some of the largest white pines on the island grow, the trees are so spaced, by natural thinning out, that a good deal of light reaches the forest floor. The response of the vegetation is immediate. Woody plants, such as seedlings of the red oak, large-toothed aspen, service-berry, white pine, gray birch, and red maple, make an understory in striking contrast to the bare condition of places where the main canopy of the white pine is dense.

Among these, and in the open places where they have not yet gotten a start, there is a conglomeration of herbs and low woody plants, which, arranged in the order of their frequency at Fawn Pond, are the following:

Gaultheria procumbens
Aralia nudicaulis
Pteris aquilina
Vaccinium pennsylvanicum
Medeola virginiana
Cornus canadensis
Trientalis americana
Clintonia borealis
Maianthemum canadense
Aster nobilis
Mitchella repens
Salix humilis
Pinus Strobus (seedlings)
Betula alba papyrifera (seedlings)
Potentilla canadensis simplex
Polypodium vulgare
Quercus rubra (seedlings)
Acer rubrum (seedlings)
Chimaphila umbellata
Amelanchier canadensis (seedlings)
Pyrola americana
Diervilla Lonicera
Lycopodium obscurum
Lysimachia quadrifolia
Viburnum cassinoides

In some parts of this growth the large aster (*Aster nobilis*), with big heart-shaped basal leaves, is locally dominant. Often it is the wintergreen or wild sarsaparilla which occupy other places to the practical exclusion of everything else.

A census of the shrubs and herbs from all the white pine localities on the island that have been studied shows that in addition to those already listed, either from Fawn Pond or Bear Brook hill, the following are at least occasionally found:

Aster acuminatus	Solidago hispida
Melampyrum lineare	Viola canadensis
Solidago bicolor	

Nearly all the herbs and shrubs that are known from the earlier developmental stages of Mt. Desert Island vegetation, and which have been already mentioned in the accounts of the rock ledges and talus slopes, and in the pitch pine, occur in similar places among the white pine. Nowhere is this so well illustrated as at Bear Brook Hill, where all stages from open rock ledges, lichen-moss carpet, pitch pine, and white pine, are to be seen growing within less than one hundred yards of one another. Wherever conditions permit, now one and now another vegetation type gains a foothold, and to avoid useless duplication, we shall not describe vegetation units that have already been noted. In all the white pine seen there are these islands, often extensive, of types of vegetation that are in more nearly the pioneer condition than the pine itself. Generally these pioneer relics are destined to change over toward more moisture-loving types of vegetation, though often because of local conditions that process may be very slow. In continuing our account of the vegetation of the island we must assume that once the types already described are fixed in the reader's mind, he will recognize them wherever they occur. As we shall see later, often rather primitive types of vegetation, due to locally unfavorable conditions, will persist for years, perhaps indefinitely, surrounded by the highest type of climax forest that the island can produce. This is particularly true in the white pine type, for while it is a valuable timber tree, and if left alone makes great diameters, it is mostly an inhabitant of poorer sites. Due to this, and to the nature of its canopy, there is more telescoping of different plant formations in it than in almost any other forest type on the island.

The white pine type occurs in the successional series on the lighter, well-drained soils. Only on abandoned clearings does it occasionally take temporary possession of heavier soils. On the lighter soils white pine reproduces well in the openings and will form an important component of the

next higher stage in the series, the mixed conifer. Its competitors, the spruce, fir and cedar, able to endure more shade, increase in proportion at the expense of the white pine, but never eliminate it because there are always openings which give it a chance.

THE MIXED CONIFER

More of Mt. Desert Island is now covered with the miscellaneous grouping of evergreens that we have called mixed conifer than with any other forest type. Always on the drier sites there is a large proportion of white pine, and on the more moist sites, spruce or cedar are more likely to dominate.

The mixed conifer is a stage in the successional series which occurs on practically all sites. Sometimes in secondary successional series, after the destruction of a spruce forest, or of a northern hardwoods-spruce forest, the mixed conifer stage may be skipped. In such cases the succession goes directly from shrubs, or from birch-aspen, to spruce or to northern hardwoods-spruce. Over most of the island the mixed conifer stage follows the white pine, sometimes directly the pitch pine, or the birch-aspen in burns. The prevalence of mixed conifer stands, and historical records of white pine in the virgin forests seen by the earliest explorers, offer a strong temptation to consider the type as a climax. Unquestionably the association maintains possession for long periods. On some of the drier sites, and rocky ledges, it may remain so long as to be a physiographic climax, or arrested stage, as with the pitch pine on Huguenot Head (Pickett Mountain). But, given centuries without disturbance, the accumulation of disintegrated rock and humus will permit the spruce, already an important component, to gain such sway as to form the true spruce type, with the white pine reduced to a small number of large conspicuous trees. On the moister sites, the succession may trend toward spruce or toward northern hardwoods-spruce, though the latter is much less common.

The proportions of the different species are extremely variable, and an average of the rather numerous counts which we have made would be misleading. In general, the proportions seem to depend on the past treatment of the forest and on the moisture of the site. On the drier and rockier sites there are fewer species, and white pine comprises a considerable proportion of the total numbers, up to 52 per cent in one case. On the moister sites there are more species, and a smaller proportion of white pine, sometimes almost none. We find hemlock, yellow birch, beech and occasionally ash. Here the trend of development may lead to the spruce climax or to the northern hardwoods-spruce climax, it is difficult to tell which, but it is probably more often the former, with, however, an admixture of hemlock and beech.

There is almost always a considerable proportion of deciduous trees, among which red oak, red maple, white birch and gray birch are the most common. The red oak occasionally attains a fair diameter, but is always short. The same is true to a less extent of the maple. None of them ever makes anything more than fuelwood. Although unimportant from the foresters' viewpoint, they must be considered in a study of the vegetation, and counted in the composition of the stand. In several cases the counting of these inferior hardwoods has brought into the mixed conifer type a stand which otherwise would have been classed as white pine. In all probability these hardwoods will diminish in proportion as the vegetation approaches more closely to the climax. The red oak will probably hold a place because of its shade endurance, as will also the beech on the moister sites. But the red maple, the birches and the aspen, being short-lived as well as unable to stand shade, will be largely eliminated except in openings which are bound to occur.

Under the canopy of this variable mixture of coniferous and deciduous trees there is, as would be expected, greater diversity of forest floor vegetation than in any other type on the island. Depending, of course, upon whether the mixed conifer is on dry or moist sites, this associated vegetation differs in its species and in the frequency of the occurrence of those plants that are found throughout the type.

In the drier places the forest floor vegetation is very much like that in the more open parts of the white pine type, which it resembles except for the larger proportion of inferior deciduous trees (red maple and birches), and of spruce. A census from several different localities shows the following shrubs as the most frequent species:

Gaylussacia baccata	Vaccinium pennsylvanicum
Kalmia angustifolia	Viburnum cassinoides

These four, with sometimes the addition of the sweet fern (*Myrica asplenifolia*), will often completely cover the ground. But it should be said that, as in other forest growths on the island, there are stretches of mixed conifer with a canopy so completely closed that there is practically no forest floor vegetation at all. In addition to these five shrubs, each one of which may be locally dominant, and a consistent mixture of which is not to be looked for, there are other woody plants that grow, almost throughout the island, in the drier parts of the mixed conifer forest. These secondary woody plants, arranged in the order of their usual frequency, are the following:

Diervilla Lonicera
Nemopanthus mucronata
Alnus mollis
Amelanchier canadensis
Pyrus americana
Rubus hispidus
Acer pennsylvanicum
Rubus canadensis
Acer spicatum

While this seems a very meager list of shrubs characteristic of such a widespread forest type as the mixed conifer, there is a possible explanation of it. As mixed conifer is developed on dry or medium dry sites it is still largely of the drought-resistant type, as evidenced by the large proportion of white and red pine in the mixture. In such places, in spite of all the accumulation of humus which must have been collected for the conifers to have developed, the site is still relatively warm and dry. The instrumental records give a fair idea of conditions in the mixed conifer type, since we know that these conditions must be intermediate between those at the white pine and the spruce stations, generally nearer the white pine. The red oak records may be considered as representing the more favorable portions of the mixed conifer type.

The herbaceous and low woody vegetation still reflects the conditions that are in a sense legacies of the pitch pine and white pine stages in the development of the forest types of the island. For the dominant herbs are, on the drier sites, still those characteristic of the drought-resistant type of vegetation. Arranged in the order of their usual frequency they are:

Aralia nudicaulis
Pteris aquilina
Polypodium vulgare
Maianthemum canadense
Aster acuminatus
Gaultheria procumbens
Cornus canadensis
Clintonia borealis
Aster nobilis
Cypripedium acaule
Chiogenes hispidula
Chimaphila umbellata
Aspidium spinulosum
Arctostaphylos Uva-ursi
Aralia hispida
Trillium undulatum
Linnaea borealis
Epipactis pubescens
Trientalis americana
Pyrola americana
Oryzopsis asperifolia
Monotropa Hypopitys
Melampyrum lineare
Vaccinium Vitis-Idaea
Lycopodium tristachyum
Epigaea repens
Viola septentrionalis

There is unmistakable evidence, however, in this list of herbs, and in the better development of the shrubs previously listed, that the mixed conifer,

even on the drier sites, marks a definite stage in the development of the vegetation. One of the most significant signs of this is the proportion of herbs that, like the orchids, shin-leaf, *Chimaphila,* Indian pipe, and the trailing arbutus, are mycorrhizal or saprophytic in their root habits. Such plants thrive only where there is considerable depth of soil and a forest canopy dense enough to make the forest floor suitable for them. While they may be found as scattered samples in a few vegetation types already noted, their occurrence for the first time in sufficient quantity to become even a small constituent of the vegetation is a pretty clear index of what the mixed conifer has done in the general scheme of the development of the vegetation.

The shrubby associates of mixed conifer on the moist sites are not very different from those listed for the drier places. One significant addition is the ground yew (*Taxus canadensis*). Not yet common is this association, its chief significance is that it is the one shrub which becomes conspicuous in the northern hardwoods-spruce, and when found it probably indicates that the succession is tending toward this climax.

The herbs of these moist sites reflect that tendency much more convincingly. While some of them are, it is true, obvious hold-overs from more pioneer conditions, others are distinctly on the side of the climax forest associates. A census of the herbs of these moist sites, arranged in the order of their usual frequency, follows:

Clintonia borealis	Osmunda cinnamomea
Aralia nudicaulis	Streptopus roseus
Cornus canadensis	Chiogenes hispidula
Linnaea borealis	Chimaphila umbellata
Gaultheria procumbens	Pteris aquilina
Trientalis americana	Cypripedium acaule
Maianthemum canadense	Polypodium vulgare
Aster acuminatus	Trillium undulatum
Aster nobilis	Habenaria orbiculata
Osmunda Claytoniana	Habenaria fimbriata

The relegating toward the end of the list of such rock and thin soil types as the bracken and polypody, and the inclusion of such a species as *Habenaria orbiculata,* shows how different these mixed conifer forests of moist sites are from the pioneer rock ledge associations. The inclusion of such a species, and the gradual fading out of once dominant drought-resistant herbs are significant milestones in the march of the vegetation toward its goal.

FIRE AND WHAT FOLLOWS

As we have shown in an earlier section of this paper, the island has been visited by disastrous fires, some of them of such severity as to completely destroy all existing vegetation. Generally speaking, fire is more apt to get a good start in those plant societies that have already been described, and in them it is quite likely to be more destructive than in those few forest types that remain to be treated.

The reason for somewhat arbitrarily placing the discussion of fire and its effects here is that among the types so far treated it is more likely to completely destroy the humus, and thus throw back the normal development of the vegetation toward the pioneer stage. In the cool and moist sites of the climax forests of spruce, and northern hardwoods-spruce, fire does not occur so often. Of course after prolonged droughts no coniferous forest is immune to fire, but generally speaking, they are in a much more fire-resistant condition than forest types with more open canopy and consequently drier conditions.

The severity of fire varies so much with the season, and its effects are so largely dictated by the wholly accidental incidence of where it starts, that it is difficult to stage a typical case. Sometimes it will sweep up a mountain side that is in one of the earlier stages of vegetative development and will succeed in merely throwing back the natural trend to some still earlier pioneer state. Again it will run through a comparatively rich coniferous woods and burn everything down to the mineral soil or rocks. Perhaps the best method is to take two areas known to have been burned over, and record what the conditions are at the present time.

In one of them, on Canada Cliff above Echo Lake, the area was burned over in the spring of 1921, and our studies of it were made in July 1922. The hill was covered originally by the climax forest of spruce, all of which with its associated vegetation was completely destroyed, as well as most of the humus. Blackened stumps on bare rocks, where the trees never could have become established without the long preparation of pioneer plants, showed how thoroughly the fire had devastated the age-long accumulation of humus, which alone could have accounted for the production of the forest on this exposed hilltop. Fourteen or fifteen months after the fire there were great stretches of bare rock, pockets of partly burned humus which had washed off the once forest clad ledges, and a good bit of mineral soil blackened by the firing of what humus it once contained.

Among all this desolation the dominant plant, making up at least seventy-five per cent of all existing vegetation, was *Aralia hispida,* which we have

seen to be an occasional inhabitant of other open places on the island, and which was dominant in a clear cutting in a spruce forest which had not been burned. On this burned area it appears at first sight as though it were the only herb, but actually there were a few other species, all of the pioneer type, growing with it. They were, in the order of their frequency, in July 1922, the following:

Pteris aquilina	Carex brunnescens
Epilobium angustifolium	Panicum subvillosum
Deschampsia flexuosa	Danthonia spicata
Carex cumulata	Polygonum cilinode
Carex Merritt-Fernaldii	Lechea intermedia
Agrostis hyemalis	Potentilla tridentata

Such a list, containing at least six species of plants not recorded from any of our forest types, and all of which are poles apart from those herbs which we know to grow associated with the spruce, is striking evidence of what fire has done. Not a single species of herb that must have been there before the spring of 1921 had survived, and this host of pioneer species had come in, to begin the slow process of building up the fertility and depth of the soil and humus so that, no one knows how many decades hence, the spruce may come into its own again.

There were a few straggling woody plants already putting in an appearance, of which the gray birch and white birch were the most common, but neither plentiful. Beside these, were occasional specimens of *Alnus mollis, Amelanchier canadensis, Acer rubrum, Myrica asplenifolia, Viburnum cassinoides, Ribes prostratum, Vaccinium pennsylvanicum, Prunus pennsylvanica,* and *Kalmia angustifolia.* All of these put together did not total five per cent of the vegetation, and, of course, all were seedlings. That the area was still a tremendous distance from such an upbuilding of its potentialities as would permit any real development of coniferous forest is obvious. Not a single evergreen seedling was found, although seed trees on a neighboring piece of unburned spruce are not too far off to preclude this. But until there has been a good deal of improvement in the site, and the birch, maple, and other woody plants have become large enough to give at least some shelter, the entrance of the spruce is probably hopeless.*

Such comparatively new burns as this one are not now easy to find on the island, as fire protection has lately become much more effective. Huge areas must have been like this years ago, judging by the great size of such places

* A careful search in 1926 on the Beech Mountain area of the same burn revealed only one small spruce seedling.

as are still marked by the vegetation that comes in after fire. While only small patches of freshly burned over areas can be found for study, hundreds of acres that were burned over years ago are now dominated by essentially pioneer growth, some of it twenty to thirty years old.

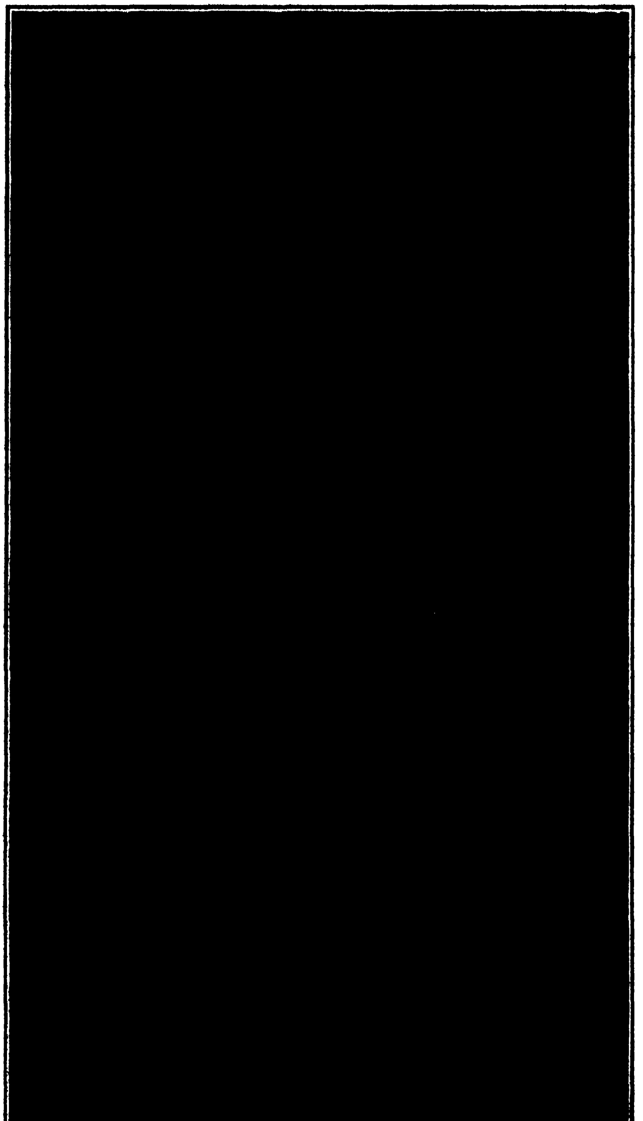

FIG. 21. White birch abo. forty years after fire, with dense understory of fir and spruce, mostly fir. Alder at edge of small opening in foreground. After the birch dies off, and the fir drops out, the spruce type will be re-established. South of Long Pond, moist site.

Our other locality for studying the effects of fire was in just this later stage. Somewhere about thirty years ago, a great fire must have swept up the north ridge of Cadillac (Green) Mountain.

On the drier parts of the slope is now a low forest of only about half density and 15 feet high composed of about 70 per cent gray birch. The remaining species and their approximate percentages are red maple 10, aspen 8, red oak 8, white birch 4. There are about 1 or 2 spruces per acre fairly well distributed, and an occasional white pine. Scattered reproduction of spruce, with a mixture of white pine, foreshadows the return of the mixed conifer type, and eventually the spruce climax.

On a moister site the trees are about 25 to 30 feet high, slightly closer, and the approximate percentages are: white birch 55, aspen 15, red maple 15, striped maple 12 (here growing in the canopy), gray birch 5, red oak 3, beech and sugar maple together 2.

These two stands of the same age, on the same burn, show pretty well the difference in composition of the birch-aspen type as influenced by moisture. On dry sites the gray birch predominates, on moist sites the white birch (Fig. 21). The tendency on some of the moist sites seems to be toward the nothern hardwoods-spruce climax.

It is needless to repeat the list of shrubs and herbs found in the beginning of forest cover under the gray birch—they are almost identical with those found on the drier sites of the mixed conifer. Under the white birch there was less forest floor vegetation owing to the closer canopy, and some of the herbs of moister sites occurred.

Several other burns were studied in different parts of the island, all of them in about the same stage of recovery as the one on the north ridge of Cadillac (Green) Mountain. So much of that recovery is due to the work of shrubs and herbs that it seems worth while to record those species that appear to play the most important part in it. Arranged in their usual order of frequency they are:

HERBS AND LOW WOODY PLANTS IN BURNS

Aster nobilis	Cornus canadensis
Pteris aquilina	Gaultheria procumbens
Aralia nudicaulis	Ribes prostratum
Vaccinium pennsylvanicum	Aster acuminatus
Solidago rugosa	Antennaria plantaginifolia
Lysimachia quadrifolia	Trientalis americana

Aster umbellatus	Lycopodium tristachyum
Polypodium vulgare	Leersia oryzoides
Rubus hispidus	Cypripedium acaule
Maianthemum canadense	Clintonia borealis
Deschampsia flexuosa	Vaccinium Vitis-Idaea
Aspidium spinulosum	

A glance at some of our earlier lists shows pretty clearly how certain of these herbs are obvious legacies of the early stages of the burn, when the whole hillside must have been more exposed than it now is. Some few of the herbs, however, as subsequent lists will show, are forerunners of the climax forest wherein they reach greater vigor and abundance.

Shrubs and Under-Canopy Trees

Diervilla Lonicera	Acer spicatum
Pyrus americana	Viburnum cassinoides
Spiraea latifolia	Myrica asplenifolia
Kalmia angustifolia	Rhus typhina
Salix humilis	Nemopanthus mucronata
Prunus pennsylvanica	Myrica carolinensis
Amelanchier canadensis	

THE HARDWOODS

Among vegetation types that are so predominantly evergreen there is only a very small place for the development of the hardwood forest, and even this, except in the northern hardwoods-spruce climax, shows signs of ultimately giving way to coniferous types. Meadow Brook is an example of hardwood containing fifty per cent of oak in its canopy, with all the rest of the canopy trees deciduous. This particular forest has already been described as our red oak station at which evaporation and soil temperature were measured (see pp. 43–45).

Under this essentially "summer forest" canopy with its lighter greens and fainter shadows there is a good development of shrubs and small trees. Seventy-five per cent of this woody growth consists of the beaked hazelnut (*Corylus rostrata*) and withe-rod (*Viburnum cassinoides*). Neither of these shrubs appears to show any preferences as to the shade of different trees under which they grow, nor as to whether they grow in openings or wholly in the shade. Associated with these two is a group of secondary shrubs, totaling about 25 per cent of shrubby vegetation. In the order of their frequency they are:

Rosa sp. (no flowers or fruit seen)	Acer pennsylvanicum
Alnus incana	Kalmia angustifolia
Diervilla Lonicera	Spiraea latifolia
Ilex verticillata	Nemopanthus mucronata
Cornus alternifolia	Rubus sp. (no flowers or fruit seen)

The frequency of relatively moisture-requiring shrubs and the scarcity of drought-resistant types are the result of the relatively favorable moisture and soil conditions at this site, conditions which have been discussed above on pages 65, 69–70, and 82–84. The herbs also reflect this, as *Aster nobilis* and *Oakesia sessilifolia* are easily dominant, especially the former which may be almost exclusive over large areas. With these two the following are found:

Aralia nudicaulis	Cornus canadensis
Aster umbellatus	Aster acuminatus
Pteris aquilina	Lycopodium obscurum
Medeola virginiana	Maianthemum canadense
Calamagrostis canadensis	Aspidium marginale
Trientalis americana	Prenanthes trifoliolata

There is a description of our station which lists (sometimes incorrectly) more species than we have included (Reiche and Burton, 1924), but does not note their frequency.

Among this aggregation of herbs and shrubs there is a vigorous reproduction of tree seedlings, and the proportion of these tells its own story of the possible permanence of the hardwood type. The percentages of different tree seedlings are as follows:

Red Oak	41.	Red Spruce	1.5
Red Maple	12.	White Pine	3.0
Service berry	11.	Fir	17.0
Aspen	1.	Ash	0.5
White Spruce	12.	White Birch	1.0

While the proportion of oak seedlings is rather high, the number of coniferous ones is significant. The fir, as commonly happens, is abundant, but will largely die out and form an insignificant part of the future main canopy. The presence of the two spruces, which stand an excellent chance of survival, and of the white pine, is significant and points to the gradual reduction of the hardwoods and the transformation of the site into a predominantly coniferous forest. It is, however, not impossible that beech and sugar maple might come in and eventually bring about the northern hardwoods-spruce climax.

9

SPRUCE CLIMAX FOREST

The spruce type has already been mentioned on page 29, and a special example in which evaporation and soil temperature were recorded has been described on pages 45 to 47. The typical spruce climax forest on Mt. Desert Island contains less fir than the one on Otter Point (Fig. 9), since the fir tends to die out as the stand becomes older. The proportion of spruce, even in the climax forest, is not uniform, varying to a certain extent with local conditions. It may run up to 100 per cent, as on Bernard Mountain (Western Peaks), which seems to be a virgin forest well representing this type. Again, it is probable that, on the drier sites, the type will always contain a certain mixture of white pine. Unfortunately, forests of this kind have all but disappeared, so we are obliged to imagine what they would be like from accounts of the early explorers, and from a few very small remnants. The spruce climax may be thought of as containing also a certain mixture of white cedar and on moister sites hemlock. In the natural openings made by the death of mature trees there would be a little white birch and aspen and an occasional red oak.

The spruce type now found on the island, except on Bernard Mountain (Western), and a few other places, is not the original forest. It is second growth which has come in as a result of cuttings which did not destroy the climax type, though they probably altered its composition to a certain extent. With this caution, we may consider it as essentially representing the climax.

Under a closed canopy of spruce the forest floor is usually entirely without flowering plants. Many parts of the island may be seen in this state or in one where herbs do not cover one per cent of the ground. Instead, there will be nothing but a carpet of spruce "duff" and sometimes on it a solid carpet of mosses with a few lichens. In this carpet of mosses the dominant and often only species is *Hypnum Schreberi*. Other mosses, hepatics and lichens are the following:

Dicranum rugosum
Dicranum scoparium
Dicranum spurium
Polytrichum commune
Ptilidium pulcherrimum
Cladonia rangiferina
Peltigera polydactyla
Cladonia gracilis elongata
Cladonia fimbriata
Cladonia pyxidata
Peltigera canina
Peltigera aphthosa
Cladonia uncialis
Cladonia sylvatica
Cladonia furcata pinnata
Crocynia lanuginosa

The richness of this moss and lichen flora is best shown where the canopy of the spruce is most dense. In stands where a little more light can get

through to the forest floor there is a small development of herbs. The dominant species are *Clintonia borealis, Trientalis americana, Streptopus roseus,* or *Cornus canadensis.* Others are, of course, found in the spruce woods and these secondary species, arranged in their usual order of frequency, are:

Maianthemum canadense, often locally dominant
Lycopodium obscurum dendroideum
Chiogenes hispidula; locally dominant under spruce at Bernard Mountain (West Peak of Western Mountain)
Linnaea borealis
Mitchella repens
Lycopodium lucidulum
Dicksonia punctilobula
Moneses uniflora
Coptis trifolia
Trillium undulatum
Monotropa Hypopitys
Aster acuminatus
Viola blanda
Cypripedium acaule
Gaultheria procumbens
Polypodium vulgare
Aralia nudicaulis
Pteris aquilina

These three do not total one per cent of the herbs

Nothing shows the great change in the environment which the spruce brings with it so much as the minor place the last three herbs fill in the forest floor vegetation. From being pioneer herbs in the open places, and occurring in decreasing frequency as the forest increases in richness, they are at last, in this climax forest of spruce, forced to the bottom of the list. And contrariwise, the plants that dominate the spruce are those that are found only sporadically, if at all, in the pioneer plant associations of the island.

Under the pure spruce stands where the canopy is somewhat open there are a few shrubs, but they appear to play a relatively minor part in the forest's economy. The following have been observed, but none of them very abundantly and most of them suppressed for lack of light:

Vaccinium pennsylvanicum
Diervilla Lonicera
Nemopanthus mucronata
Viburnum cassinoides
Vaccinium Vitis-Idaea
Vaccinium canadense

Except the first and last, these shrubs are more tolerant of shade than any others on the island, but even these make up scarcely five per cent of the total forest floor vegetation under the spruce. The blueberries are sparsely

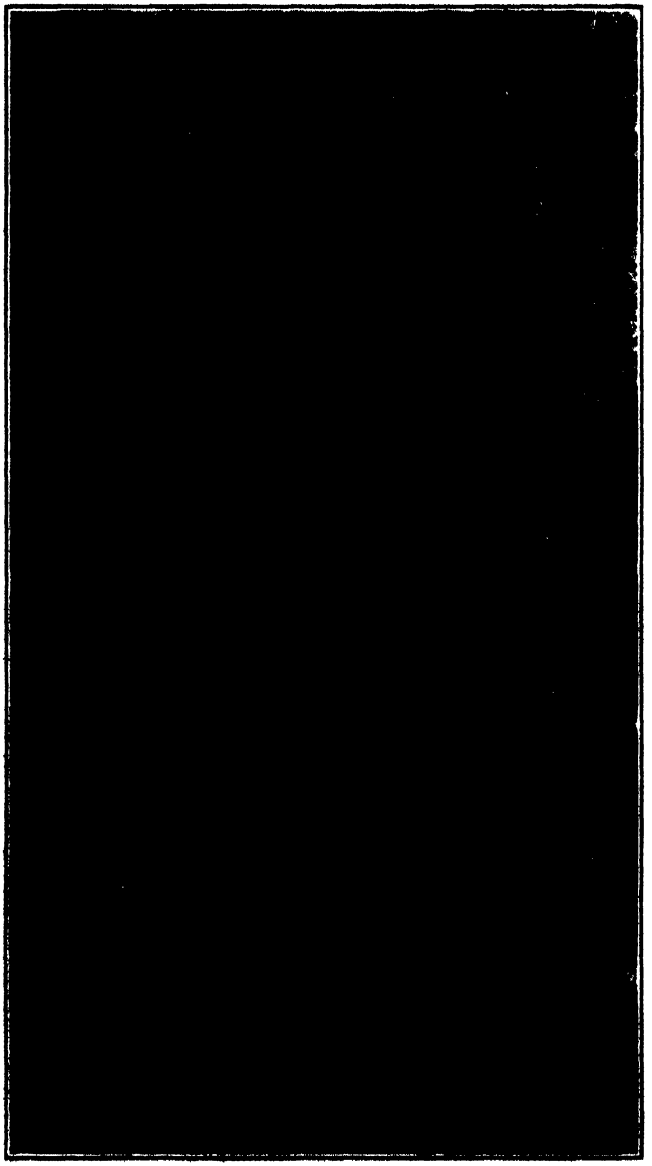

FIG. 22. Northern hardwoods-spruce type south of Bubble Pond, second growth. Right (with cap) yellow birch, next sugar maple, beech in background, spruce on left and spruce saplings. Much young sugar maple reproduction. This spot is mapped as hardwoods, because most of the spruce has been removed. See text page 30.

scattered, and perhaps remnants of or intruders from some earlier vegetation type.

Perhaps the outstanding feature of the associated vegetation of these climax spruce forests is the paucity of herbs and shrubs. There is the same paucity among the pioneer plant societies of the rock ledges; but, while in that case the unfavorable factors are heat, exposure, and too high evaporation, in the spruce it is just the reverse. In these cool, moist, sombre forests, the crowding of the canopy is so complete that little or no sunlight ever gets to the ground. The resulting sparseness of forest floor vegetation is striking.

NORTHERN HARDWOODS-SPRUCE CLIMAX FOREST

No other forest on Mt. Desert Island can compare with the northern hardwoods-spruce (Fig. 22). Instead of the sombre shade of the spruce woods, there is golden-green light, and over many square rods the large irregular patches of the evergreen yew with its cheerful red fruits. There is real beauty in these woods, with their combination of "summer forest" and constantly changing lights and shades, as these are determined by the mostly deciduous canopy and the darker shadows of the occasional spruces. While the type covers thousands of square miles of the mainland, there are only a few places on Mt. Desert Island on which it shows good development.

The dominant species are the three characteristic northern hardwoods, beech, yellow birch and sugar maple, with an admixture of red spruce. Hemlock is common, though forming only a small percentage. The hornbeam (*Ostrya virginiana*), which, though small, sometimes extends up into the main canopy, is characteristic of this type of forest. There are occasional species from other types, such as white birch (common at the margin of the type), a little red oak and an occasional red maple.

The great difference between the density of this canopy, as compared to the pure spruce or to the mixed conifer that contains a good deal of spruce, is reflected in the under vegetation. As a record of what occurs in this climax forest the following list is presented, which comprises a census of all the plants observed in the few places where the northern hardwoods-spruce is found. They are arranged in the order of their frequency:

Herbs
- Clintonia borealis
- Trientalis americana
- Aspidium spinulosum intermedium
- Aralia nudicaulis
- Medeola virginiana
- Aspidium marginale
- Mitchella repens
- Streptopus roseus
- Lycopodium lucidulum
- Aster acuminatus

Smilacina racemosa
Polypodium vulgare
Maianthemum canadense
Oxalis Acetosella
Cornus canadensis
Polygonatum biflorum
Solidago latifolia
Trillium undulatum
Polystichum acrostichoides
Oakesia sessilifolia
Aster nobilis
Gaultheria procumbens
Coptis trifolia
Actaea alba
Osmunda cinnamomea
Galium triflorum
Monotropa Hypopitys
Pteris aquilina
Pogonia verticillata
Pyrola americana
Monotropa uniflora
Pyrola secunda
Cypripedium acaule
Habenaria macrophylla
Corallorrhiza maculata

The profusion and variety of herbs is obviously greater here than under the canopy of any other forest type on the island. And on this herb-strewn forest floor are two shrubs that are easily the dominant woody plants. Nowhere else on Mt. Desert Island are the hobble bush (*Viburnum alnifolium*) and the ground yew (*Taxus canadensis*) so common as in these northern hardwoods-spruce forests. Sometimes they are the only woody plants beside the canopy trees. Usually, however, there are other species, which, arranged in the order of their frequency, are:

Acer spicatum
Acer pennsylvanicum
Lonicera canadensis
Amelanchier canadensis
Amelanchier oblongifolia
Corylus rostrata
Pyrus americana
Nemopanthus mucronata
Vaccinium pennsylvanicum
Cornus circinata

THE RÔLE OF CERTAIN MT. DESERT PLANTS IN THE DEVELOPMENT OF THE VEGETATION

Before passing to the stages of plant succession which start in water or on wet sites, it is worth while to consider a few of the many species of plants in upland associations, and to follow briefly the fortunes of these plants in the stages of development of the vegetation from the open rocky sites to the climax forests.

In the accompanying chart (Fig. 23) twenty-two species have been plotted as to their frequency, dominance or waning in the different plant associations of the uplands. Each of them is dominant in some association of plants, but only two are found in every association, *Vaccinium pennsylvanicum* and *Polypodium vulgare*. These two are thus the most widely dispersed

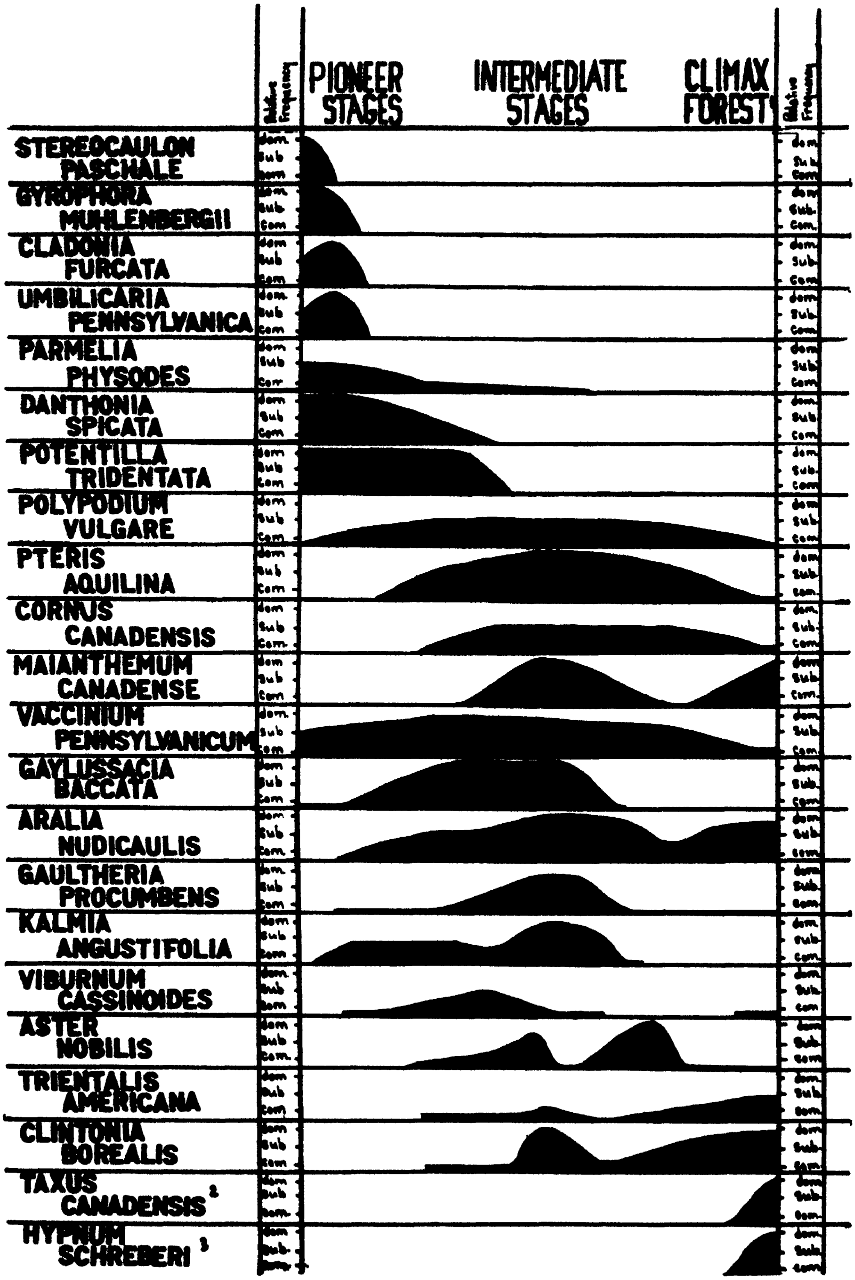

FIG. 23. The rôle of 22 Mount Desert plants in the development of the vegetation. Chart showing relative frequency in: (*a*) the pioneer stages, which are mostly on bare rocks, and the earliest aggregations of plants that grow on such places; (*b*) the intermediate stages, where there is a distinct forest cover, still mostly or in some part dry conditions; and (*c*) the climax forest. In the abbreviations under "Relative Frequency," "dom." = dominant, "sub." = subdominant, "com." = common.

Notes: 1. Climax forest is of two types in different parts of the island, spruce and northern hardwoods-spruce.

2. *Taxus canadensis* is dominant only under the northern hardwoods-spruce climax.

3. *Hypnum Schreberi* is dominant only under the spruce climax.

plants on the island, other than forest trees. In the case of the blueberry, the typical form is sometimes replaced by *Vaccinium pennsylvanicum angustifolium*, but both the blueberry and the polypody are very common all over the island. *Polypodium vulgare* is of some phytogeographical significance, so far as its occurrence on Mt. Desert is concerned, for it is widely distributed throughout the north temperate zones of Europe, Asia, and at least eastern America, as well as in certain regions in the southern hemisphere. Such nearly cosmopolitan distribution argues a wide degree of variability and adaptability, which on a small scale is reflected in the plant's occurrence over so much of the island.

The low blueberry, which also runs the gamut from extreme drought-resistant to the most moisture-requiring types, is a native species of much more restricted general distribution. The typical form is recorded, in Gray's Manual, from Newfoundland to Saskatchewan, south to Virginia, Illinois and Wisconsin. Some of its forms may extend its geological or altitudinal limits a bit, but this "lowest and earliest ripened of the blueberries" is essentially a plant of northeastern America. Its striking frequency all through the earlier pioneer and semi-dry stages is not so surprising as its persistence through to the moist spruce and northern hardwoods-spruce. In both the latter it is much reduced in volume due to the density of the canopy, but it still makes up some slight proportion of the total vegetation in both types.

While the blueberry and polypody are, par excellence, the most adaptable of all the associated plants on the uplands, there is a group of species that is very nearly as general in its distribution and sometimes even in its frequency. Of these the all but world-wide bracken (*Pteris aquilina*), the wild sarsaparilla (*Aralia nudicaulis*), and perhaps the black huckleberry (*Gaylussacia baccata*) are the most important. In the case of the bracken, there is scarcely a part of the globe suitable for plants where this fern is not found.

Gaylussacia baccata and *Aralia nudicaulis* are in a very different category. Both are nearly the commonest associates of the pitch pine over hundreds of square miles of the hot coastal plain from Long Island southward. Both of them, again according to Gray's Manual, find their northern and eastern limits in Newfoundland. And both are, under all the more open-canopied forest types of Mt. Desert Island, among the most plentiful of the associated plants. Both reflect the curious anomaly of an island whose forest destiny is unquestionably of the northern and consequently spruce type, and because of the very incomplete nature of the fulfillment of that destiny is carrying along a group of species that is progressively reduced as the climax is approached. All three of these plants, as well as others too numerous to mention, and of which these are merely examples, are hardly to be expected

in significant quantity under a mature canopy of the climax spruce. And, while some of them are found there at the present time, their survival is perhaps best accounted for by considering them as mere *survivors* of earlier forest stages, or as plants that are driven from opening to opening as fire or natural destruction of the canopy gives them a precarious chance to snatch such opportunities.

The first seven species on the chart (Fig. 23) are predominantly of the pioneer type, and, so far as our records show, do not occur at all beyond the intermediate stages of succession, which may be considered as the mixed conifer of medium or dry sites. In the case of *Potentilla tridentata* we have a plant, which, while commonly associated with the plants already mentioned, is of different origin and distribution from the black huckleberry and wild sarsaparilla. The three-toothed cinquefoil is a plant that nearly always inhabits rocks, instead of the sands and gravels of the coastal plain, and its range is from "Labrador to eastern New England, where common in exposed rocky or gravelly situations, New Jersey, and southward on the upper Alleghenies; also westward, chiefly along the Great Lakes." It is nowhere recorded from the coastal plain, and yet on this island its nearly universal associates are three or four species that find their greatest development outside of Mt. Desert Island, on the coastal plain.

At the other end of the chart are those species that one would expect in an essentially northern flora, and their occurrence in both the climax forests is what is to be expected.

Their inclusion, however, in forest types a good way short of the climax, which the chart shows, and which many observations on other species confirm, may be considered simply as an example of the intermixture of plants having vastly different origins. It is this phenomenon, more than anything else, that makes the vegetation of the island so well worth preserving. For as the years go on, later students may perhaps actually catch distributional trends in operation, of which these preliminary notes and records are obviously only a hint.

STAGES ORIGINATING IN WATER

Although covering less area than the upland associations, the stages of development originating in water are interesting and important. It will be seen from the chart (Fig. 14, p. 86) that the trend of development seems to be largely controlled by drainage. The species which establish themselves where there is a more or less constant flow of water are not those which can endure the highly acid conditions resulting from stagnant waters which develop into true bogs. On the drained sites we find marshes, passing over into

swamps—red maple or white cedar (*Thuja occidentalis*). Some of the marshes may, however, pass into bogs with interruption of drainage due to the accumulation of vegetation or other causes. A good example is seen in Northeast Meadow on the northern edge of the island. Here large stretches are hardly above high tide level, but protected from the bay by surrounding upland through which Northeast Creek has cut a relatively narrow channel. Although the water is brackish far up into the meadow, two miles and more from the mouth of the stream, yet acid-tolerant bog plants are invading the meadow and extending to the very edge of the alkaline water. While the main drainage of the meadow is good, its flatness and large size do not permit of sufficient flow, aside from the main stream and tributaries, and therefore give a chance for the accumulation of acid and the encroachment of bog plants. This meadow will therefore pass through the true bog stages, and already affords an excellent opportunity for studying this kind of development, as well as salt marsh stages and well-drained marsh.

It is probable that deficient drainage is not the only factor that distinguishes bogs from wet areas of low acidity. Just what the other factors are we are not yet in a position to state definitely. But the character of the substratum seems to play a part. Under the bogs there generally seems to be a considerable depth of sphagnum peat, with little or no mineral content, indicating the former presence of water that was at least not shallow. On the other hand the wet areas of low acidity, such of them as were observed, had mineral soil near the surface. This mineral soil was in some cases a fine grey or bluish silt or clay, probably of marine origin and neutral in reaction, and in others it was a neutral gravel. In Great Meadows just north of the Sieur des Monts Spring the outer or southern margin of the meadow is neutral, and is covered with luxuriant grasses and red maple. Here the underlying vegetable matter—a shallow layer of decomposed grasses, not sphagnum—rests on a fine gray neutral silt or clay. Further out in the meadow, where the water of the former lake must have been deeper, the substratum is a mass of highly acid peat of unknown depth. Thus it seems reasonable to conclude, at least provisionally, that depth as well as drainage determines whether a water area shall become an acid bog or a neutral swamp.

Poor Drainage—Bogs

Undrained or poorly drained areas of considerable size occur, still in the stage where there is complete exposure to sunlight and no trees. All the true bogs are practically without free drainage of their water, which, as it is squeezed out of the sphagnum sponge, always shows a high degree of acidity. So great is this that only typical bog plants are found in such places at first,

and it takes a considerable time for it to build up to the stage where acid-tolerant trees can get a foothold.

There is a marked similarity between the different bogs on the island, as the ecological conditions in them are so nearly uniform. The same herbs and shrubs, in practically the same mixture, will be found over many acres, even in widely separated localities. In fact few plant societies appear so stable and monotonous as bogs, although it is true that they contain a group of species found rarely, if at all, in other parts of the island, and are but a stage between open water and the climax forest.

FIG. 24. Excellent example of stages in bog succession from open water to trees. Lily pads (*Nymphaea advena*) on left, with sphagnum under and around the pads; floating mat of sphagnum with a scattering growth of sedges. On right is shrub stage, *Myrica gale* and *Kalmia polifolia*; on extreme right are small black spruces. Sunken Heath, near Youngs Corners.

Where open water still remains, there may be a slight development of true aquatic vegetation, the commonest species of which are *Nymphaeà advena*, *Brasenia Schreberi* and *Potamogeton epihydrus* (Figs. 24 and 25). None of these aquatic plants is common, and they do not, in the big pools examined on the island, make any such growth as similar ecological plant societies in coastal plain bogs.

Along the edges of the pools there is an abundant development of matted sphagnum (Fig. 24), the three commonest constituents of which are

Sphagnum papillosum, *S. pulchrum* and *S. Warnstorfii*. This sphagnum mat may be at the level of the water, or above it, according to the stage of de-

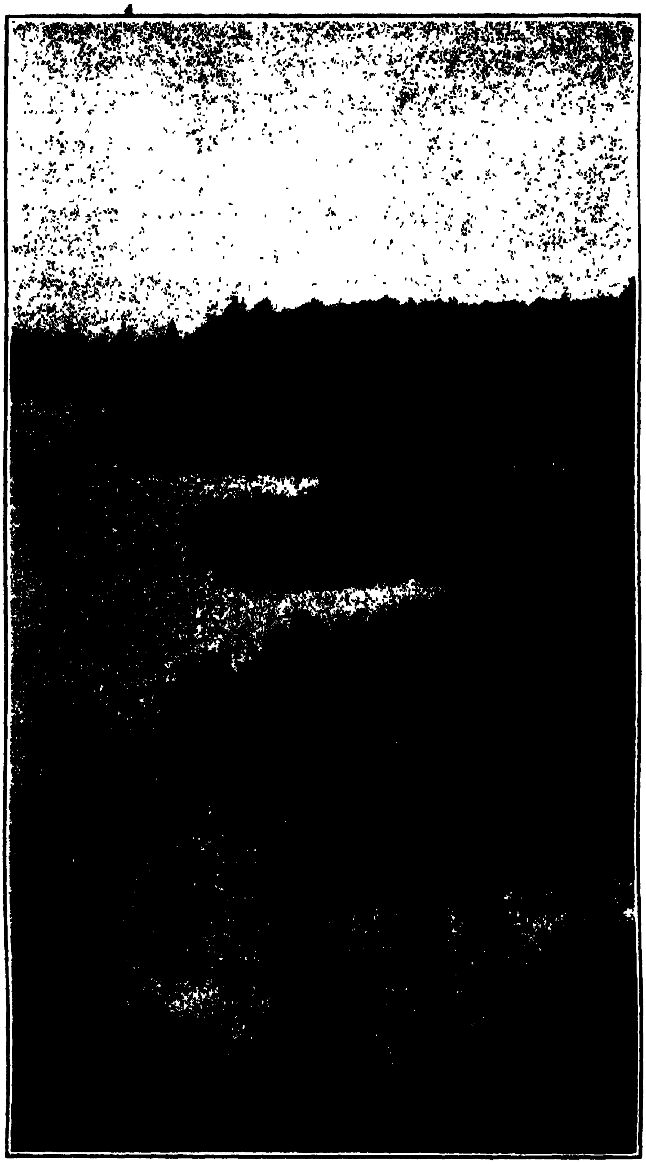

FIG. 25. Shrub stage in contact with open water. Lily pads in water. Shrubs are *Chamaedaphne calyculata* and *Kalmia angustifolia*. Mat of *Empetrum nigrum* under shrubs, and a few pitcher plants (*Sarracenia purpurea*). Sunken Heath.

velopment, and may be up to five feet wide, though generally much less, depending upon the depth of water. It varies as to width, and in some places

it has an intermixture of sedges or shrubs which characterize a later stage in development of bog vegetation.

Where there is any considerable belt of sphagnum we find the beginnings of the establishment of certain plants which in later stages cover much of the bog to the exclusion of practically all other plants. One of the most frequent of the pioneer flowering plants to get a foothold on the moss carpet is *Rynchospora alba;* another is *Scirpus caespitosus callosus.* While, in the earlier stages, neither of these does much more than dot the sphagnum with a few isolated samples, a little later, at least *Scirpus caespitosus callosus* becomes very plentiful. It is a common sight to see acres covered by this sedge, with practically no woody plants among it, and almost no other herbs.

Before, however, reaching such a predominantly sedge stage, the pioneer sphagnum mat is more apt to have growing with these scattered sedges the following, arranged in the order of their usual frequency:

Eriophorum callitrix	Drosera rotundifolia
Carex rostrata	Drosera longifolia
Solidago uniligulata	Aster nemoralis
Eriophorum virginicum	Scheuchzeria palustris
Sarracenia purpurea	Utricularia cornuta

None of these is common enough to make up any such large growth as *Scirpus caespitosus callosus,* and most bogs have only a limited development of this herbaceous growth, and that, of course, only in their younger stages.

The next stage is the covering of this herbaceous vegetation by woody plants, or the shrub stage (Figs. 24, 25 and 26). Where this has gone on for a long period the sphagnum and the herbs will be much reduced, and in the case of the moss, there is, after years of building up, a gradual decay. In this sponge of moss, sometimes lichen covered, the typical bog shrubs get a foothold, and from that time on the growth of sphagnum or herbs is a rather precarious matter. When, as often happens, the shrub growth becomes exclusive and very dense, there will be no moss or herbs visible. Actually, of course, this never happens over a whole bog, as there are always openings for one reason or another, where shrubs fail to develop, and sphagnum and herbs go on monopolizing areas that are not yet ready for shrub growth.

The dominant shrubby species in the bog is easily the leather leaf (*Chamaedaphne calyculata*) which over many acres may grow almost to the exclusion of everything else. More often, however, it has scattered through it other species, some of which are often plentiful enough to be locally dominant. These associated shrubs are:

Kalmia angustifolia
Rhododendron canadense
Ledum groenlandicum
Myrica Gale
Kalmia polifolia
Andromeda glaucophylla
Viburnum cassinoides
Gaylussacia dumosa
Pyrus melanocarpa
Vaccinium Vitis-Idaea
Vaccinium Oxycoccus
Empetrum nigrum
Nemopanthus mucronata
Alnus incana

FIG 26 Forest invading the shrub zone Black spruce, with a mixture of larch Sunken Heath

All of these, except the second, are either naturally low shrubs or are so affected by the acidity of the bog that they do not grow more than a foot or two high. In this nearly exclusive shrubby growth, but sometimes in places where the bog is still dominated by the sedge, *Scirpus caespitosus callosus*, there are many tree seedlings. At first these tree seedlings are mostly all black spruce (*Picea Mariana*) or larch (*Larix laricina*) (Fig. 26). White pine has however been found in the early stages of bog succession rather abundantly, though stunted and with short yellowish needles.

The interesting merging of bog vegetation with the typical flora of the salt marshes in Northeast Meadows near Eden has already been mentioned. The marsh-bog-upland area covers many acres, all the salt water end of the region being dominated by such plants as *Spartina Michauxiana, Spar-*

tina patens, Triglochin maritima, Carex Oederi pumila, Plantago decipiens, Potentilla Anserina, and near the edges by *Solidago sempervirens.* Where the specific gravity of the water in the stream (corrected to 60° F.) is as high as 1.0186, *Spartina Michauxiana* makes up ninety-five per cent of the vegetation, and down near the tidal inlet where the specific gravity varies from 1.0220 to 1.0224 it is the exclusive plant.

Toward the upper end there is a progressive dying out of this salt marsh flora, the most striking evidence of which is the almost complete disappearance of *Spartina Michauxiana.* At this point the water has a specific gravity of 1.0105. Here the development of *Calamagrostis canadensis* becomes striking, and where the water approaches neutrality this grass covers much of the marsh.

Once this stage is reached, and the general floor of the marsh is built up high enough to be above the influence of the highest tides, a typical bog flora begins to get a foothold. The acidity of this bog muck was found to be as high as any inland bog, and like those, there is already evidence, from larch, spruce, white pine and white birch seedlings, that ultimately forest growth will capture the place.

Good Drainage—Cedar Swamps

Wet areas where the drainage is good pass through somewhat different stages from those described for bogs, because there is not as much accumulation of acid. At first the water plants are not very different from the poorly drained series. But instead of a mat of sphagnum we find the second stage made up of tall luxuriant grasses, soon followed by alder and soft maple. High bush blueberry (*Vaccinium corymbosum*), though not abundant, is found here.

An important stage in the succession on some, perhaps not all, well-drained wet places is the cedar (*Thuja occidentalis*), a typical example of which is shown in figure 27. In pure or practically pure stands cedar generally grows in swamps, but sometimes is found on steep rocky slopes, as on the west side of Sargent Mountain. As a constituent of most forest types on the upland it is one of the most widely distributed trees on the island. It never attains large size except in the cedar swamps and in moist hollows where the soil is neutral or of low acidity. Cedar groves are as dense canopied as the spruce, especially in young stands where the trees may be so close together that walking is difficult. Even more mature groves are very dense (Fig. 27) and in some of them there is practically no forest floor vegetation.

The composition of the canopy trees of a typical mature stand in a cedar

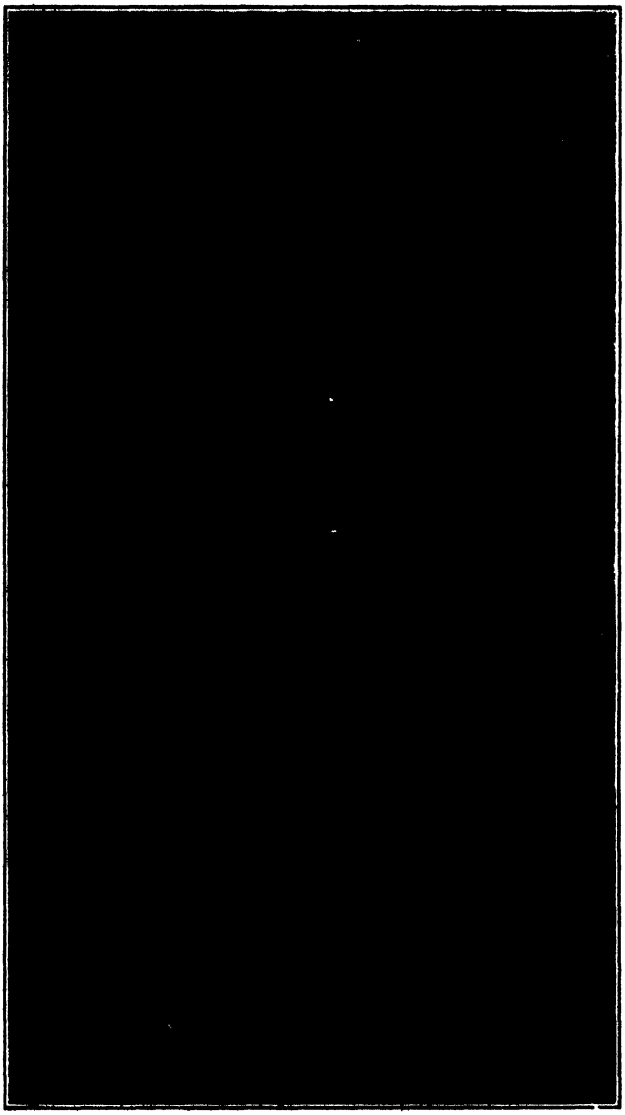

FIG. 27. A mature cedar swamp, about 100 years old, southeast of Aunt Betty Pond.

swamp, east of Squid (Goosemarsh) Cove, was found by actual count to be as follows:

White cedar	87.8	per cent
Spruce	6.3	"
Yellow birch	3.1	"
White pine	1.6	"
White birch	.8	"
Fir	.4	"

In other cedar swamps, ash, both the white (*Fraxinus americana*) and the black (*F. nigra*), are not uncommon.

The reproduction in dense cedar swamps contains a large number of one year old cedar seedlings, but not many older ones, indicating low survival. More significant are the seedlings of fir, spruce, and even white pine, which manage to survive at least a few years under the heavy shade.

The presence of spruce, fir and white pine in the main canopy, and in the reproduction, may mean that eventually the cedar swamps will develop into the mixed conifer type, and then into either the spruce or the northern hardwoods-spruce climax. The occurrence of yellow birch and of yew may indicate a leaning toward the latter. There is a constant accumulation of humus which eventually builds a substratum high enough above the water to permit sufficient aeration for the roots of the spruce and pine. The process is, however, slow.

Under the densest canopy there may be no flowering plants, and mosses carpet the ground, especially the mounds that are almost universally found around the tree trunks. Some of these hummocks around older trees may rise as much as two feet above the general level of the swamp, and the smooth rounded surface of nearly all of them is dominated by one species of moss, *Hylocomium proliferum*. In much smaller volume are *Sphagnum capillaceum* and *Sphagnum squarrosum*. Over the general level of the swamp *Mnium cinclidioides* and *M. punctatum* are easily dominant, but mixed with them are *Thuidium delicatulum* and *Mnium affine*, together with those species already noted on the hummocks.

If the canopy is not too dense this moss-covered forest floor may have a few herbs, or even a scattered clump or two of ground yew (*Taxus canadensis*), but such associated vegetation would not ordinarily cover one tenth of one per cent of the forest floor. The plants that manage to persist are usually

Osmunda regalis
Cornus canadensis
Viola pallens
Carex leptalea
Coptis trifolia
Chrysosplenium americanum
Chiogenes hispidula
Maianthemum canadense
Rubus hispidus
Viburnum cassinoides
Dalibarda repens
Clintonia borealis
Trientalis americana
Listera cordata

PRACTICAL CONSIDERATIONS IN FORESTRY

The practical applications of the results of the foregoing study of the vegetation of Mount Desert Island properly belong under technical forestry, landscape architecture, and the various applied sciences which make use of ecological information in their practice. We will here confine ourselves to outlining briefly some of the more general practical considerations in the field of forestry, on which the results have a bearing.

Much of the land on Mt. Desert Island has a value which is based not only on its capacity to produce farm crops or timber, but on its desirability for summer cottages or other recreational purposes. Obviously this added value makes it unprofitable to acquire the land as an investment in timber production. But, for those who hold the land, and do not expect to sell it in the near future, a revenue from timber, when compatible with the other uses, means just so much reduction in the cost of carrying the land.

It is worth while emphasizing here the fact that, aside from virgin forests of large trees which in themselves constitute a major scenic attraction, a reasonable amount of cutting under proper forestry methods does not injure the beauty or attractiveness of the forest. On the contrary, such treatment distinctly improves it by removing the half dead unsightly trees, and giving a chance to the thrifty younger ones. Tree growth on the island is so abundant that the forests are too thick and the trees kill each other. The result is stagnation of growth and injury to all. Eventually some win out and continue to grow, after having lost much time and often suffered more or less severely in the intense struggle. All this can be avoided by judicious thinnings at the proper time.

In the past the value of the wood has not been sufficient to warrant much expenditure in producing it. But prices have now reached a point where they amply justify at least simple cultural operations such as thinnings, particularly when these thinnings pay for themselves, or even yield a profit, in the form of poles, fence posts, fuelwood, or even pulpwood. It is also not improbable that the prices will be even higher in future.

The climate and soil over most of the island are such that the trees do not grow tall and straight, as they do under more favorable surroundings. The section on the environment gives a little idea of some of the more important conditions. Therefore, it will not be possible, except on certain small areas,

to produce high grade timber. But the growth in diameter is fairly rapid, and the yield per acre will probably be fairly high. No figures have been secured to show how much this would be, but a rough guess would place it at around 300 board feet per acre per year, or even more with intensive forestry. Furthermore, natural reproduction of the more valuable species is unusually plentiful and easy to secure. Hence it will practically never be necessary to incur the expense of planting.

Most of the island is easily accessible, transportation offers no difficulties, and markets are good. In fact, the island has been producing timber practically ever since it was settled by white men. But the forests have been abused or neglected so that the yield is but a small fraction of what it would be under even the simplest and crudest sort of care.

People have been learning that it is more profitable to work with nature, than to ignore it. We may think that a certain kind of tree is more rapid growing and more valuable than the one which naturally thrives in a certain place, and so try to eliminate the native one to make way for the more valuable. Cases of the kind are numerous, but it is only in recent years that the consequences are beginning to make themselves felt. An example which will serve to illustrate the point is found in the artificial spruce forests of Saxony in Germany.* The yield tables showed that artificial spruce forests produced 69 cubic feet per acre per year. Since this was highly profitable, large areas were planted to spruce. Now they find that nature is asserting itself. The spruce needles have caused leaching of the soil and lowered its fertility. Exposure at the times of clear cutting has packed the soil and caused poor aeration. Disease has come in. The result has been a drop from 69 to 40 cubic feet per year, and serious losses for the overconfident and grasping owners.

Another example is the experience on the Harvard Forest at Petersham, Massachusetts. The high returns on white pine made it appear desirable to grow this tree everywhere. But it was found that on the heavier soils, in spite of the fact that they now bear white pine, the tree does not reproduce itself and does not do well. It took possession of these sites when the cultivated land was abandoned at the time of the westward migration after the Civil War, but is a temporary stage in the succession leading to the deciduous climax forest. Fighting nature was found to be a poor investment, and the attempt was abandoned in favor of methods based more nearly on the natural course of events. The later methods have proven highly successful as well as profitable.

In like manner on Mount Desert Island, it will pay to handle the forests

* Journal of Forestry **21**: 718–722. 1923.

in such a way as to follow or work in with the developmental trends of the vegetation rather than against them.

At the present time white pine is the most valuable and most rapid growing tree on the island, or for that matter in all New England. The aim should be to maintain as large a proportion of this species in the stand as possible. The foregoing investigation has shown that the white pine and mixed conifer types are merely stages in the successional series leading eventually to the spruce climax forest, or less frequently the northern hardwoods-spruce. Our object then should be to intervene at the proper moment in such a way as to induce nature to continue the largest possible proportion of white pine in the stand. This involves handling the forest in a way which will make conditions unfavorable for invasion by spruce and fir. Since the latter species can stand more shade than white pine, we can probably maintain the white pine on suitable sites by making openings of the proper size several years before the stand is finally cut. In the cold shore zone we might as well accept the inevitable and give up the white pine in favor of the spruce, itself a valuable tree.

Should we wish to replace the white pine by spruce for any reason, it will not be difficult since we are following the usual trend. We can let the canopy close up and remain fairly dense, not a difficult matter except on the very dry and rocky sites.

It may be unnecessary, but will avoid misunderstanding, to point out that the above suggested forestry methods do not apply to the Lafayette National Park. The purpose of the Park is to preserve a beautiful spot in an absolutely natural condition for the enjoyment of future generations, and for science and education. It is a place on which the native plants and animals may be found undisturbed by outside agencies. When all else around it is artificial, the National Park will be natural. On it the forces of nature which have been described in the foregoing pages will be left to work out the ultimate destiny of the vegetation without human interference. Future generations will be able to profit by the mistakes of the present, and will know exactly what changes take place. Thus the National Park, when kept intact and free from the introduction of exotic plants or animals, or other well-intentioned but potentially disastrous human interference, will continue to give inspiration through its beauty and through its wealth of scientific materials as yet almost unexplored.

SUMMARY

Mt. Desert Island, Maine, is of exceptional scientific interest as a meeting ground of northern and southern forms of both plants and animals. We are here concerned only with the plants and their environment.

The chief rock formation of the island is granite, which has been left after ages of erosion as a relatively high range extending in a southwesterly-northeasterly direction across the island, and attains an elevation of 1532 feet at its highest point. Glaciation has cut the range into a number of more or less isolated peaks with their long axes running approximately north and south. But the mountains still act as a barrier across the island sufficient to create noticeably different conditions on the northern as compared with the southern parts of the island.

After the last ice retreat the island was submerged to approximately 210 feet below its present level.

The soils are of glacial origin except for marine clays and silts deposited during submergence. The chief soil is a reddish brown glacial till, more or less stony, which on certain slopes below 210 feet has been somewhat reworked by wave action. Deposits of sand and gravel occupy a relatively small proportion of the island. Pockets of blue marl and of a fine grey silt cover considerable areas below the 200 foot contour. The hills are largely without soil, and characterized by large expanses of bare granite, varying from perpendicular cliffs to rounded domes.

A distinct layer of raw humus or "duff," unmixed with the mineral soil, overlies most of the surface except for certain moist and sheltered valleys where decomposition keeps pace with formation so that the humus goes into the soil. In places this humus blanket has been burned off by past fires, exposing the bare rock and soil.

The coastal plain plants which form such an unusual and interesting component of the vegetation probably reached the island by way of a land bridge formed by an extension of the coastal plain above the sea from New Jersey to Newfoundland.

Previous to its settlement by white men, the island had been repeatedly subjected to fire by the Indians to drive out the game. When discovered by Champlain in 1604 the summits were bare rock, and the forest contained tall pines standing above the main canopy of spruce and fir, with white birch in mixture. Even before its permanent settlement, the annals of which begin

only in 1762, timber was cut on the island. Logging operations, principally for small mills, have continued practically uninterruptedly to the present day, and timber has been one of the chief products of the island. Fires, many of them sweeping over large areas, have been so frequent that there is hardly a spot on the island which has not been burned since its settlement. Lately, fires have been controlled and largely prevented. Most of the burned lands are restocking naturally with conifers under the birch and aspen, but there are also large stretches with practically nothing but worthless stunted grey birch. These will eventually come back to coniferous forest, given long enough under protection from fire.

The vegetation is predominantly northern, with an admixture of southern elements. Red spruce is easily the principal tree in point of numbers and distribution over the island. White pine is also very abundant. White spruce is unusually plentiful for this latitude, especially in the forests near the sea. White cedar (arborvitae) is everywhere, but attains good development only in restricted spots. The white birch, red oak, red maple, and gray birch are about equally abundant, though varying in amount on different sites. Beech, yellow birch and sugar maple are restricted to the more favorable places.

The largest area, aside from burns, is covered by a variable mixture of the foregoing conifers and deciduous trees, which we have called the mixed conifer type. But here and there representative examples of the principal forest types of New England, and of the pitch pine barrens in New Jersey, crystallize out of the mixture and afford an unusual opportunity for studying the environmental conditions controlling the existence of forest types elsewhere found in widely separated localities.

The forest types are: spruce, 70 per cent or more of red or white spruce or both, corresponding with the "spruce slope" type of inland Maine, the White Mountains and Adirondacks; northern hardwoods-spruce, beech, yellow birch, sugar maple, and spruce, corresponding with the most widely distributed forest type of northern New England; white pine, 70 per cent or more white pine, corresponding with the commercially most important type of central New England; white cedar swamp, 80 per cent or more of white cedar; and lastly pitch pine, 80 per cent or more pitch pine. There is also on Acadia (Robinson) Mountain an extremely interesting isolated but vigorous growth of scrub oak (*Quercus ilicifolia*), here at or near the northern limit of its range. If we include the mats of the arctic alpine crowberry (*Empetrum nigrum*) along the shore, we have represented a stretch of country extending from Labrador to New Jersey. Furthermore, the representation is

not merely by isolated specimens interesting principally to collectors, but by vigorous self-perpetuating types of vegetation (associations).

The total precipitation, 48.3 inches, the mean annual from 1886 to 1908, is ample for luxuriant vegetation, but is not very well distributed, only one third, exclusive of the amount from melted snow, coming in the growing season. In summer, periods of prolonged drought are not uncommon. The temperature is uniformly low, a mean annual of 44.0° F., with a monthly average of 21.0 for the coldest month, January, and only 65.5 in July, the warmest month. The average length of the growing season is 126 days, from May 18 to September 24.

Records were secured with simple instruments which gave an indication of the moisture and temperature conditions under which four forest types are growing. These types were (1) spruce, (2) red oak, (3) white pine, and (4) pitch pine. Though typical of widely separated regions, the stations themselves were all within 4 miles of each other, on sites of markedly different physiography.

For a general index of moisture conditions, evaporation was measured during the summers of 1921, 1922 and 1923 with Livingston atmometers, both white and black spheres being used so as to obtain solar radiation. Bates inner cell evaporimeters were also used part of the time, in these three years, and in 1924. As an index of temperature relations, we recorded maximum and minimum soil temperature at 6 and 18 inch depth during the summers of 1922 and 1923. Evaporation was secured both under the canopy in each of the four types and in the open, to give conditions which the forest had to overcome to become established. Soil temperatures were recorded under the forest only. Readings were made weekly during June, July, August and September. Synchronous readings in a pitch pine forest on Long Island were obtained for comparison.

Perhaps the most striking, anyhow the most unexpected, result of the instrumental records was the discovery that evaporation on Mt. Desert Island, in spite of the markedly colder temperature, proximity to the sea, and lower wind velocity, is consistently much higher than on Long Island. This seems to be due to the surrounding cold sea water, which lowers the capacity for moisture on the part of the air passing over it, often causing fogs. On striking the sun-heated expanses of rock this air rises in temperature before it can take up a corresponding amount of moisture, and therefore has a low relative humidity as it passes over the island. Later, in moving inland it picks up moisture from lakes and vegetation, so that evaporation inland in Maine is much lower than on Mt. Desert Island.

The records covered two very dry years, 1921 and 1923, and one wet

year, 1922. The relationships between the four forest types, both as to evaporation and temperature, were consistent throughout. In the wet year (1922) the average daily evaporation at the open stations was: pitch pine 27.7, white pine 23.4, red oak 17.2, spruce 16.4. Under the forest it was: pitch pine 16.6, white pine 11.6, red oak 5.3, spruce 4.0. In a dry year (1923) in the open, it was: pitch pine 37.3, white pine 30.7, red oak 24.7, spruce 21.4. Under the forest it was: pitch pine 24.3, white pine 17.4, red oak 8.5, and spruce 7.0 On Long Island the pitch pine in these two seasons showed 26.2 and 22.1 in the open, with 11.9 and 12.1 under the forest.

The ratios, in 1923 in the open, on the basis of Mt. Desert pitch pine as 100, were as follows: pitch pine Mt. Desert 100, pitch pine Long Island 59, white pine 82, red oak 67, spruce 57. In the forest they were pitch pine Mt. Desert 100, pitch pine Long Island 50, white pine 72, red oak 35, spruce 29. The ratios in 1921 and 1922 were practically the same as in 1923, except that in 1921 the red oak open station was proportionally higher, 77 instead of 67, but in the same position in relation to the other types.

The soil temperature differences were of less magnitude than those of evaporation, but the stations stood in the same order. In 1922 the mean temperature at 6 inches in degrees F. was: pitch pine 58.0, white pine 56.0, red oak 55.7, spruce 53.4. The ratios on the basis of pitch pine as 100 were only: pitch pine 100, white pine 97, red oak 96, spruce 92. The spruce represents the cold shore zone.

The 18 inch readings showed that at this depth the soil temperature under the forest, even on markedly different physiographic situations, is practically the same except for the greater cold of the spruce type near the sea. Even that is only 5 per cent lower than pitch pine (51.6 as against 54.4).

The soil temperatures in 1922 and 1923 were remarkably similar.

The mean soil temperatures at 6 inches under pitch pine on Long Island were, in 1922, 7.4 degrees higher than under the Mt. Desert pitch pine, and in 1923, 6.8 degrees higher. At 18 inches Long Island was 9.8 higher in 1922, and 12.3 higher in 1923.

The records show that evaporation and soil temperature are higher in the type representing the most southerly geographic region (pitch pine) and decrease going northward. The environment is very unfavorable in the pitch pine forest, owing to excessive atmospheric dryness, and is favorable in the spruce.

The red oak type studied appears to be a temporary stage leading to the mixed conifer type, and eventually to the spruce climax. The records for the red oak are intermediate between those of the white pine and spruce, and

probably come within the range of conditions under which the mixed conifer forests are growing on the island.

As an index of the physical properties of the principal soils, the wilting coefficient was determined by the direct method. Soil acidity was found by the Wherry field method of color indicators. Nitrogen analyses made by Wherry gave an indication of soil fertility, which was further tested by cultures of corn, spruce and fir on soils from five of the more important forest types. The differences in the wilting coefficients and acidities do not appear to correspond with differences in forest types, except that the white pine type is restricted to the lighter soils. The white cedar swamps seem to be correlated with a low degree of acidity.

The nitrogen analyses showed that the soils under the deciduous forests, except the red oak type, had a higher nitrogen content than the coniferous forests. The northern hardwoods-spruce type is due to higher soil fertility as well as to greater moisture, and perhaps in part also to shelter from the sea winds. The spruce type grows on soils very low in nitrogen, provides its own nitrogen in the humus, and is probably controlled more largely by climate than by soil. The pitch pine type grows on very poor soil, and is confined to the drier and warmer sites. White pine soils contain moderate amounts of nitrogen, and are fairly fertile, as well as being porous. The red oak type is due to a moderately fertile soil, and probably in part also to poor soil aeration, which excludes the conifers until the soil has been improved by the accumulation of humus.

Two climax forest types are recognized as the ultimate vegetative cover, given sufficient time without disturbance. These are spruce over most of the island and northern hardwoods-spruce on restricted areas. The succession of the vegetation is shown in a chart (Fig. 14, p. 86).

The development of the vegetation from bare rock with south exposures to the climax forest of the island goes through the following series of stages: (1) lichens, (2) lichen-moss mat, (3) shrubs (with also herbs), (4) pitch pine forest, (5) white pine, with or without red pine, (6) mixed conifer, (7) spruce climax. Sometimes one or more stages are omitted or "telescoped." On north slopes or level places it goes through: (1) lichens, (2) lichen-moss mat, (3) shrubs, (4) mixed conifer, (5) spruce.

On particularly unfavorable sites, as for example Huguenot Head (Pickett Mountain), the development may be arrested, or may be so slow that the pitch pine forest becomes for all practical purposes a physiographic climax. The same may be true of the scrub oak on Acadia (Robinson) Mountain

On light soils the series is: (1) shrubs, (2) pitch pine, (3) white pine, with or without red pine, (4) mixed conifer, (5) spruce, or possibly (5)

northern hardwoods-spruce. Sometimes the pitch pine stage is " telescoped." On heavier soils the series is shorter, from (1) shrubs to (2) red oak and red maple, (3) mixed conifer, (4) spruce or northern hardwoods-spruce.

The water series depends on drainage, and possibly also depth of the water. With poor drainage and deep water it becomes a bog series from: (1) aquatics to (2) sphagnum-sedge, (3) spagnum-shrub, (4) black spruce, (5) mixed conifer, (6) spruce or northern hardwoods-spruce. With good drainage and shallow water it is: (1) aquatics, (2) sedge, (3) alder, (4) red maple, (5) mixed conifer, (6) spruce or northern hardwoods-spruce. Or it may go from (2) sedge to (3) cedar swamp, (4) northern hardwoods-spruce directly, or (4) mixed conifer and (5) northern hardwoods-spruce or spruce.

For 22 species the frequency, and rôle in the different plant associations, aside from the water series, has been given graphically in a chart (Fig. 23, p. 129). The first seven species are the pioneers, coming into the early stages of the vegetation, and at the other end are those which would be expected in an essentially northern flora, and which here occur in the climax forests.

The results of the study serve a practical application in forestry in indicating trends of vegetation, and enabling us to partially guide the natural course of events rather than to work against it with the inevitable disastrous consequences.

The application does not include the Lafayette National Park, which, when all else around it becomes artificial, will remain the one spot on which the forces of nature will have an opportunity of working out the ultimate destiny of the vegetation and wild life without human interference.

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BROOKLYN BOTANIC GARDEN

MEMOIRS

VOLUME IV

TWENTY-FIFTH ANNIVERSARY PAPERS

PRESENTED MAY 15, 16, 1935

PUBLISHED MAY 7, 1936

BROOKLYN, N. Y., U. S. A.

LANCASTER PRESS, INC., LANCASTER, PA.

In Grateful Appreciation
This Memoir is Dedicated to
the Memory of
ALFRED TREDWAY WHITE
(1846–1921)

INTRODUCTION

The Twenty-fifth Anniversary of the Brooklyn Botanic Garden was celebrated on May 13 to 16, 1935. Special programs suitable to the occasion were arranged for each of the four days. A special Commemoration Program was held on Monday evening. The Twenty-first Annual Spring Inspection took place on Tuesday afternoon. On Wednesday there were three sessions, morning, afternoon, and evening, devoted to a Scientific Program, the underlying theme of which was the progress of botany during the period 1910–1935. On Thursday morning a Horticultural Program was given, and Thursday afternoon and evening were devoted to an Educational Program.

The detailed programs are outlined on the following pages.

On Monday evening, following the Commemoration Program, there was a reception to members and guests by the Trustees and the Woman's Auxiliary. Invitation buffet luncheons were furnished on Wednesday and Thursday. The Junior League of Brooklyn was hostess at a tea on Thursday afternoon, and on Thursday evening there was an informal reception with the Brooklyn Botanic Garden Teachers' Association as hostess.

The success of the meetings was due in large part to the active participation of the Woman's Auxiliary of the Botanic Garden; the publication of the scientific and horticultural papers was also made possible by its contribution of funds for that purpose.

COMMEMORATION PROGRAM

Monday Evening, May 13, 8:30

FORMAL EXERCISES FOR OFFICIALS, GARDEN MEMBERS, AND INVITED GUESTS

Presiding: MR. EDWARD C. BLUM
President of the Board of Trustees

INTRODUCTORY REMARKS

MISS HILDA LOINES
Chairman of the Botanic Garden Governing Committee

ANNOUNCEMENTS

DR. C. STUART GAGER
Director, Brooklyn Botanic Garden

GREETINGS

For the City of New York

HON. RAYMOND V. INGERSOLL
President of the Borough of Brooklyn

For the Department of Parks

HON. ROBERT MOSES [1]
Commissioner of Parks, New York City

For the Educational Institutions

HON. GEORGE J. RYAN [2]
President of the Board of Education

Address: Botany and Human Affairs

DR. ALBERT F. WOODS
Director, Graduate School, U. S. Department of Agriculture

[1] Unable to be present.
[2] Represented by Dr. Jacob Greenberg, Associate Superintendent of Schools, Board of Education.

TWENTY-FIRST ANNUAL SPRING INSPECTION

Tuesday Afternoon, May 14

FOR OFFICIALS, MEMBERS, AND INVITED GUESTS

Guest of Honor: HON. FIORELLO H. LAGUARDIA
Mayor of the City of New York

The guests, accompanied by members of the Garden personnel as guides, were conducted in groups of convenient size on a tour of inspection of the grounds.

ITINERARY

1. The Japanese Garden.

2. Cherry Walk and the flowering trees adjacent.

3. The Overlook from which a view may be had of

4 The Horticultural Section, recently graded and partially planted this spring.

5. The Local Flora Section, containing only plants that grow wild within 100 miles of Brooklyn.

6. Return past the Rose Garden and Lilies-of-the-Valley to the Laboratory Building.

Following the tour of inspection, tea was served in the Laboratory Building by the Woman's Auxiliary.

SCIENTIFIC PROGRAM

Wednesday Morning, May 15, 10:30

Presiding: R. A. HARPER, *Emeritus Professor of Botany, Columbia University*

1. VIRUS DISEASES OF PLANTS: TWENTY-FIVE YEARS OF PROGRESS, 1910–1935
   L. O. Kunkel, *Head of the Division of Plant Pathology, Rockefeller Institute for Medical Research, Princeton, N. J.*
2. TWENTY-FIVE YEARS OF CYTOLOGY, 1910–1935
   Charles E. Allen, *Professor of Botany, University of Wisconsin*
3. TWENTY-FIVE YEARS OF GENETICS, 1910–1935
   Albert F. Blakeslee, *Director, Department of Genetics, Carnegie Institution of Washington*

Wednesday Afternoon, 2:45

Presiding: EDMUND W. SINNOTT, *Professor of Botany, Barnard College. Columbia University*

1. TWENTY-FIVE YEARS OF PLANT PHYSIOLOGY, 1910–1935 [1]
   Rodney H. True, *Professor of Botany and Director of the Botanic Garden, University of Pennsylvania*
2. LIGHT ON VEGETATION, 1910–1935
   John M. Arthur, *Boyce Thompson Institute for Plant Research*
3. TWENTY-FIVE YEARS OF ECOLOGY, 1910–1935
   H. A. Gleason, *Head Curator, New York Botanical Garden*
4. TWENTY-FIVE YEARS OF FORESTRY, 1910–1935
   Samuel N. Spring, *Dean, New York State College of Forestry, Syracuse University*

Wednesday Evening, 8:15.

Presiding: WILLIAM CROCKER, *Director, Boyce Thompson Institute for Plant Research*

1. TWENTY-FIVE YEARS OF PLANT PATHOLOGY, 1910–1935 [2]
   L. R. Jones, *Professor of Plant Pathology, University of Wisconsin*
2. TWENTY-FIVE YEARS OF SYSTEMATIC BOTANY, 1910–1935
   Elmer D. Merrill, *Director, New York Botanical Garden*
3. TWENTY-FIVE YEARS OF PALEOBOTANY, 1910–1935
   G. R. Wieland, *Associate, Carnegie Institution of Washington*
4. MOTION PICTURE (SILENT). THE LIFE CYCLE OF A FERN. 2 Reels, 35 mm. Harvard Film. Premier Showing.

[1] The paper by Prof. Rodney H. True was transferred to the evening session.
[2] Prof. L. R. Jones was unable to be present.

HORTICULTURAL PROGRAM

Thursday Morning, 10:30

Presiding: John C. Wister, *Secretary, The Pennsylvania Horticultural Society*

1. Twenty-five Years of Horticultural Progress, with Special Reference to Foreign Plant Introduction, 1910–1935

   W. E. Whitehouse, *Senior Horticulturist, U. S. Department of Agriculture*

2. Opportunities for Women in Horticulture, 1910–1935

   Kate Barratt, *Principal, The Swanley (England) Horticultural College*

3. Growing Plants in Sand with the Aid of Nutrient Solutions: with Special Reference to Practical Applications

   C. H. Connors, *Head of the Department of Floriculture and Ornamental Horticulture, New Jersey Agricultural Experiment Station*

4. Modern Methods of Plant Propagation

   P. W. Zimmerman, *Plant Physiologist, Boyce Thompson Institute for Plant Research*

5. Plant Patents

   Robert Starr Allyn, *Deputy Commissioner of Sanitation, New York City*

6. Motion Picture. Naturalized Plant Immigrants

   U. S. Department of Agriculture, Bureau of Plant Industry. 2 Reels.

EDUCATIONAL PROGRAM

Thursday Afternoon, 4:00

Presiding: JOHN S. ROBERTS,[1] *Associate Superintendent of Schools, New York City*

1. BOTANICAL EDUCATION FOR YOUNG PEOPLE

   D. W. O'Brien, *Assistant Director, Department of Manual Arts, The School Committee of the City of Boston*

2. TWENTY-FIVE YEARS OF BOTANICAL EDUCATION, 1910–1935

   Otis W. Caldwell, *Professor of Education, Teachers College, Columbia University*

3. MOTION PICTURE. HOW SEEDS GERMINATE

   U. S. Department of Agriculture, Bureau of Plant Industry. 1 Reel.

Thursday Evening, 8:15

Presiding: JULIUS M. JOHNSON, *President, The New York Association of Biology Teachers*

1. ADULT EDUCATION IN BOTANY

   Loren C. Petry, *Professor of Botany, Cornell University*

2. RADIO IN BOTANICAL EDUCATION

   Morse Salisbury, *Chief of Radio Service, United States Department of Agriculture*

3. MOTION PICTURES: THEIR PART IN AMERICAN EDUCATION

   Clarence E. Partch, *Dean, School of Education, and Director of the Summer Session, Rutgers University*

4. DEMONSTRATION OF SILENT "MOVIES" AND "TALKIES"

   a. Time-Lapse Studies in Plant Growth. 1 Reel.
      U. S. Department of Agriculture Film.

   b. Plant Life (A Sound Film). 1 Reel.
      Harvard Film Service.

[1] Dr. John S. Roberts was unable to be present. Dr. P. W. Zimmerman, Boyce Thompson Institute for Plant Research, presided.

EXHIBITS

Exhibits illustrating the scientific and educational activities of the Brooklyn Botanic Garden were set up in the corridors, lecture rooms, laboratories, and conservatories as follows:

BENEDICT, RALPH E. Boston fern development.

BEST, JULIA E. Venation in leaves of cotton.

BUHLE, LOUIS. Enlargements of portraits of botanists.

CHENEY, RALPH H. The Genus Coffea.

CHICHESTER, EMILIE P. Books and manuscripts illustrating history of botany.

CONKLIN, MARIE E. Root nodule bacteria.

CURRIE, JAMES N. Algae cultures.

DONEY, CHARLES F. Malus species. (Watercolor drawings by Maud H. Purdy.)

DORWARD, MARGARET M. Class work throughout the year. Instruction Greenhouse.

FREE, MONTAGUE. Plant propagation. Conservatory.

—— Horticultural awards to Brooklyn Botanic Garden.

GAGER, C. STUART, AND MONTAGUE FREE. Development of Brooklyn Botanic Garden illustrated by photographs. (Enlargements by Louis Buhle.)

GRAVES, ARTHUR H. Chestnut breeding.

GUNDERSEN, ALFRED. Flower structures and the classification of Dicotyledons. (Drawings by Maud H. Purdy.)

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BOTANY AND HUMAN AFFAIRS[1]

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"Botany and Human Affairs" is a rather broad subject to present in twenty-five minutes. But I am advised by Director Gager that various special phases will be discussed in detail by other speakers, so that I may confine my remarks to a more general treatment of the larger aspects of the subject, creating, if you please, a background for the real pictures to come later in this program.

All animals, including man, are dependent for food directly or indirectly on some form of green or chlorophyll-bearing plant life. The study of these organisms, that make man's life possible, is of as great fundamental importance as the study of man himself.

Botany in its broad sense is the systematized knowledge we possess of the vegetable kingdom as a whole. It includes all that is known about plants, their history through the ages, as we get it in geology and paleontology, the description and classification of all known forms of living plants; the study of their origin, life relationships and development (embryology, genetics); their structure (histology and cytology and morphology); their physiology, their composition, modification, mutation and evolution; their cultivation, propagation and breeding; their diseases, their relation to each other and to other organisms and to the factors of their environment. From the economic aspect it is evident that this includes much of agriculture, forestry, horticulture, pharmacognosy, floriculture and cognate subjects.

At the lower end of this great kingdom of plant life we find the beginning of what we know as living organisms, those complex molecules that we call protoplasm, that are able under favorable conditions to sustain and reproduce themselves from the inorganic elements of their environment, the so-called autotrophic microorganisms. These are the simplest types of living organisms. Some of them are so small that they are invisible under the highest powers of the microscope. Others are more like fungi or algae without

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chlorophyll, though some of them do contain chromogen materials. The energy that they need for their life processes they are able to draw from the inorganic materials of their environment, from combinations of nitrogen, phosphorus, sulfur, chlorine, potassium, calcium, magnesium, iron, copper, manganese and possibly a few other elements. This ability to extract energy from inorganic compounds, utilizing it for the reduction of carbon dioxide to organic compounds, is limited to a very few species, but they are of very great importance in soil formation and in soil fertility. They include such genera as *Nitrosomonas, Nitrosococcus,* which oxidize ammonia to nitrite, *Nitrobacter,* which oxidizes nitrite to nitrate, and species of the genus *Thiobacillus,* which oxidize sulfur and its compounds, utilizing also light energy. Others oxidize iron and manganous compounds and others oxidize hydrogen. Some of these contain pigment and may be algae rather than true bacteria.

Then comes the great group of microscopic parasitic and saprophytic *heterotrophic Bacteria.* We know now as a result of the facts brought to light by those who study these forms of plant life that they bring about fundamental transformations and changes necessary to the existence of higher forms of life. In association with other plants or plant remains some of them oxidize atmospheric nitrogen into nitric acid and ammonia in forms available to higher plants. Some of them have formed cooperative or symbiotic relations with higher plants, as for example with Leguminosae, the alfalfas, clovers, peas, beans, which are among our most valuable soil-building and feed and food crops. They prepare the food material for higher plants. They separate these materials again when the plant or the animal that feeds on them dies. Others have become parasitic, causing disease and destruction to higher plants or animals. Crown gall or plant cancer, pear blight and various rots and wilts, some extremely destructive, are examples of plant diseases caused by bacteria. Tuberculosis, anthrax, tetanus, typhoid fever, cholera, pneumonia are among the well-known and destructive animal diseases caused by bacteria.

In this same general group of parasitic and saprophytic organisms are the fungi, yeasts, moulds, rusts, smuts, toadstools, mushrooms, bracket fungi, and hosts of others, some helpful and valuable, others harmful and causing destructive diseases of plants and animals. This group is especially prolific in species causing plant diseases. Some of the most destructive and best-known examples are the black rot of grapes, bitter rot of apples, apple scab, peach and plum rot, the fusarium wilts of cotton, flax and cow peas; the root rot of corn and the scab of wheat and barley; the rusts and smuts of wheat and other cereals and a great variety of other plants; the mildew rots of grape, potato and hops; the heart rots of trees and various root rots; chestnut blight and Dutch elm disease.

Most of these fungi have complicated life histories living in different forms on totally unrelated plants. One form, or stage, of the black rust of cereals, for example, lives only on certain species of barberry (*B. vulgaris* group), from which it moves again to the cereal host. The blister rust of the white pine passes part of its life on gooseberry and currant leaves. The unraveling of these life histories is the most effective means to a knowledge of effective control.

The black rust of wheat of the bread varieties can be controlled in part by destroying the common barberry (*B. vulgaris*) in the regions where these wheats are grown. The blister rust of white pine can not be prevented, except by destroying the gooseberries and currants in the vicinity of white pines. These are simply two well-known examples of hundreds of other similar associations, some with plants and some with insects, highly important to our welfare to understand. Dr. Geo. M. Reed, of the Brooklyn Botanic Garden, is doing some outstanding work on smut diseases of cereal grains. These diseases are very destructive and difficult to control. Dr. Reed has discovered the existence of physiological races or varieties of smuts. Varieties of the parasite that look exactly alike under the microscope may be quite different in their ability to infect a particular strain or variety of grain. These facts must be taken into consideration in breeding for resistance to smut infection. The smuts cause enormous losses in a great variety of cereals. The work that is being done here by Dr. Reed in cooperation with the United States Department of Agriculture is of very great scientific as well as of very great practical value in giving us increased power to protect our most important food crops.

The average annual loss to our crop plants caused by diseases alone averages 10 per cent, or more than $500,000,000 a year. All our botanical research in this field costs less than one tenth of one per cent of the annual saving from the application of its results. A careful estimate made in 1928 covering about 40 years of research by the Bureau of Plant Industry of the U. S. Department of Agriculture in cooperation with other agencies in the general field of applied botany showed an annual saving and gain of more than $500 for every dollar expended.

Let us move upward now on the ladder of life from the lowest forms of plant life to those organisms that are more commonly known as plants, *viz.*, those organisms that are green. They differ from the bacteria and fungi in that they are able to live normally only in the light. They draw their energy from the sun, utilizing it to combine carbon dioxide with water, forming starch, sugar and cellulose, freeing bound oxygen in the process which adds materially to our slowly waning atmospheric supply. They then bring about com-

binations of sugar and nitrate or ammonia forming albuminoids and proteins, which are the basis of protoplasm, both in plants and animals. Plant and animal life, except the small group of bacteria able to obtain their energy from inorganic sources would be impossible without this fixation of carbon and transformation of energy carried on by green plants. Some of these green plants are so small that they are invisible to the unaided eye, single cells no larger than some of the bacteria. These are the simple algae, furnishing foods for other forms of microscopic aquatic animal life, which in turn are the food of forms of increasing size and complexity, and finally for oysters, lobsters, crabs and fish and other forms of aquatic animal life. Others are banded together into great masses of surprising beauty, like the sea weeds. Others are the grass of the field, which " to-day is and to-morrow is cast into the oven " or dies down to enrich the soil for the corn and wheat, the vine and the fruit tree or the great trees of the forest.

Plants are the great soil-builders and protectors of soil from wind and water erosion. Where we have destroyed vegetation planlessly and thoughtlessly we are rapidly losing our soil by wind erosion in dry periods and by water erosion in wet periods. In the last few years the topsoil on millions of acres west of the 100th meridian has been blown away in dust storms. Millions of acres have been covered by windblown sand. This is largely the result of overgrazing and consequent destruction of the plant cover or destruction of the plant cover by breaking up the sod to prepare the land for wheat or other crops. The danger has been appreciated by botanists and agriculturists for many years. But their warnings have not been heeded. Experiment stations established in this dryland area two decades ago have studied these problems and have pointed out safe uses for these lands, but lack of general appreciation of the danger has prevented general adoption of the methods recommended. The situation is now so serious that the whole nation is awake to it. Our botanists, ecologists and agriculturists are striving to find soil-binding plants and methods of checking erosion and in a measure repairing the damage. Botanical explorers are visiting various parts of the world to find additions to our store of drought-resistant and soil-binding plants to aid in this recovery program. Many valuable wild and cultivated species are being introduced. Botanic gardens furnish extremely valuable help in this and other plant introduction work.

In the areas formerly forested a similar process of unwise destruction of the forest cover has been going on for many years. Land of little or no value for agriculture has been denuded of its trees through destructive lumbering followed by fire. The exposed soil has been washed into the streams, choking their channels. Heavy rains are followed by floods. Navigation

and power resources are destroyed. The aquatic plants are destroyed, followed by the animal life, fish and game when their primary food source is gone. The whole balance of nature is thus upset. What was once a source of wealth, and under proper use would have continued to be such, is rapidly becoming a barren waste and a source of danger. The indiscriminate dumping of sewage and industrial wastes into streams, lakes and the ocean is rapidly destroying aquatic vegetation of all types beneficial to aquatic animal life and the source of their food supply. Oysters, clams, crabs, fish and waterfowl disappear with their food supply. The public does not yet understand this danger to our great natural aquatic resources, and destruction still goes on. Here is a great field for the botanist and zoologist to do effective research and educational work. It is encouraging to note that the Secretary of War has appointed a committee to look into this pollution problem.

A program of erosion control has been recently inaugurated in a large way, and reforestation, range control on the public domain and land use programs are now matters of national concern. Intelligent plans are being made to correct these maladjustments as rapidly as possible. Botanical knowledge and research are the keys to the solution of these great problems. In this new era botany in its broad sense will be called upon to play an increasingly important part in the re-establishment of biologically balanced areas. The ecologists and physiologists have a large part to play. The plant explorers have important contributions to make. The phytopathologists must be on the job. There is work for the expert systematists, the algologists and bacteriologists, as well as foresters and agronomists. In all this work botanic gardens and arboretums will prove to be of increasing value.

With careful study and planning we shall be able in many cases to improve on the former natural vegetation. In many cases we shall use our rapidly increasing knowledge of genetics to breed and fix better varieties and strains of plants better adapted to special uses—plants that are more resistant to drouth and cold, more firmly and deeply rooted, more resistant to disease and insect pests, and of better or more desirable quality for uses to which they may be put. All these things are now being done by botanists. Gradually through botanical study we have learned some of the secrets of making new varieties and species and establishing and even patenting some of them.

The plant breeder could not exercise this power to produce and establish new varieties with the efficiency now attained had not the student of genetics made available a large fund of information in this special field of research. The story is a long one, starting with the discovery of the sexuality of plants by Camerarias in 1691. Probably the most important discovery was that of Gregor Mendel more than 70 years ago in regard to the law of the distribu-

tion of unit characters in the progeny of hybrids. With improved technique and equipment it is possible now to connect certain characters of the progeny with the genes (the hereditary units) of the chromosome controlling those particular characters. It may be possible in the future to more definitely control the combination of different genes to produce the new varieties of plants, having the combination of the characters desired. This is now accomplished by crossing large numbers of individuals having the unit characters desired, then selecting and recombining until the desired result is obtained. By taking advantage of the Mendelian formula, the fixed strains of the desired type if produced may be segregated in three generations, provided further crossing is eliminated. By using these methods the rust and drouth resistance of macaroni wheats (*Triticum durum*) have been successfully combined with *T. vulgare,* the ordinary bread wheat. At the wheat-breeding station at Omsk, Russia, the bread wheats have been successfully crossed with a wild grass, *Agropyron elongatum,* transmitting drouth, rust and alkali resistance to the progeny. Wilt resistance of the citron has been bred into the watermelon. The resistance of certain Asiatic chestnuts to chestnut blight has been bred into the American chestnut. Almost every variety of cultivated crop has been improved in one or more particulars by plant breeders. Some fine work of this kind is in progress here. Dr. Graves, of the staff of this garden, for several years has been collaborating with the Federal Department of Agriculture in producing hybrids between the American and Japanese and Chinese varieties of chestnuts, with a view to producing a tree which will not only be immune to chestnut blight, which has almost exterminated the American chestnut, but will also be a valuable timber tree. The results strongly indicate that this much-desired objective will be accomplished. Botanic gardens and arboretums are especially valuable as sources of breeding material and as centers where such studies can be carried on. They are among the most important sources of living plant material and are invaluable centers of technical and practical information in every phase of botanical study in its broadest sense. We need more of them and we should give them better financial support. Aside from their generally recognized practical value, they have great civic and educational value especially to the community in which they are located. Another line of development is the artificial production of mutation (inheritable variation not the direct result of crossing) by exposing the reproductive cells to x-rays and similar types of radiation. Profound changes are produced in this way.

Dr. Gager, the director of the Brooklyn Botanic Garden, shortly before coming to Brooklyn conducted extensive pioneer studies on the effect of the rays of radium on the various life processes of plants, and since coming to

Brooklyn he has collaborated with Dr. Blakeslee, of the Carnegie Institution of Washington, in exposing reproductive cells to radium rays. The result of this work was to produce probably for the first time inheritable changes in living organisms by exposing their living cells to penetrating radiation. It is epoch-making work and is a field worthy of most careful study. Then there is the newly discovered mode of germplasmic origin of new characters *aristogenes,* of which at present we have no control.[2]

By varying the length of exposure to light and by modifying the wave-lengths of the light used or by increasing or decreasing the intensity of the total light and modifying the periods of exposure we can produce profound changes in the time of flowers and fruiting. This method of control has already proved to be of great value in plant breeding in the control of flowering periods and it may have much wider use, especially in plant introduction and adaptation. Changes in chemical composition, especially the vitamin content, may be brought about by light control. This vitamin content of plant tissue is especially important. The vitamins appear to be of the nature of vegetable hormones, certain of them controlling growth in animals; others control lime assimilation, reproduction and resistance to disease. This is one of the most productive and active fields of plant physiological, biochemical and biophysical research at the present time. It is opening a new field of nutrition and health preservation and control and prevention of some of the most serious diseases of man and other animals, such as tuberculosis, beriberi, scurvy, rickets, xerophthalmia, pellagra, rheumatism and others.

The ultra-violet rays are principally involved in vitamin formation. These rays are largely eliminated by ordinary glass. Leafy field crops, like lettuce, grown under ordinary glass, should therefore receive supplementary ultra-violet light treatment if their vitamin content is to be up to normal. Special glass transmitting these rays is now available but at considerably increased cost. · Special ultra-violet light radiation equipment is also available.

The environmental, nutritional and genetic factors controlling the production in the plant of other valuable organic constituents—gums, oils, fats, alkaloids, rubber—are still very imperfectly understood and offer a productive field of great scientific and economic value. Here again botanic gardens and arboreta afford the most helpful aids to such investigations. Time does not permit multiplication of examples of how botany, a knowledge of plant life, in one way or another enters into almost every aspect of our welfare. The time allotted might easily be consumed in the more detailed presentation of some narrow field, but I have selected the more general and less technical

[2] Science 80: 604, December 28, 1934.

presentation so that those of you who are not botanists may get the broader perspective of the relation of botany to human welfare.

In closing this presentation I wish to give you an illustration of the importance of intensive study of problems that may appear at first sight to have no possible value to humanity. Botanists, as well as other scientists, are frequently criticized for devoting too much time and money to what the critic considers to be quite useless and worthless but which may later prove of very great value. There are numberless examples. I have time to call your attention to but one in which the Bureau of Plant Industry of the U. S. Department of Agriculture found uses for an apparently unimportant discovery made by Karl Wilhelm von Nägeli, a brilliant Swiss botanist. Von Nägeli, desiring to study under the microscope the activities of living plant cells, selected for the purpose what is popularly known as " frog spittle " or " green slime," a fresh-water alga belonging to the genus *Spirogyra*. This alga grows in ponds and slow streams and looks to the naked eye like fine, long, green silk threads. The microscope shows that the thread is made up of large cylindrical cells attached end to end, having spiral bands of chlorophyll. The protoplasm and nucleus show clearly. It is thus easy to see the living cell in operation. This, of course, was the reason for selecting this plant for study. It might not have appealed very strongly to the visiting committee of farmers and business men or the president of the university had they happened in at that time. They probably would have been more disgusted than was Nägeli himself when he could not get the alga to grow in his carefully prepared synthetic solutions, containing everything needed by the alga in just the right proportions. Day after day he tested and retested to find the reason why the *Spirogyra* died in his aquarium but would live in the water brought in from the pond containing the same nutrient salts. In his synthetic solutions made up from distilled water and from tap water, the *Spirogyra* after a few hours turned brown, broke up into short pieces and in twelve to twenty-four hours was dead. To make a long story short he finally traced the cause of death to minute traces of copper taken up from the bronze faucet in his laboratory as the water passed through it. The amount of copper was so small that it could not be detected by any chemical method known. But the chlorophyll band in the *Spirogyra* cell reacted to one part of copper in 50 million parts of water. It thus proved to be the most sensitive test known for copper. He described his researches and published them in a little pamphlet which remained untranslated and almost forgotten for more than half a century.

The next chapter in the story opens with a letter received by the Department of Agriculture from a cress grower, who complained that he and others

growers were being put out of business by some disease attacking the cress. As this was quite an important industry in which many millions of dollars were invested, we sent Dr. George T. Moore to investigate. He found that the trouble was caused by *Spirogyra* smothering the cress. He thought right away of the work of Nägeli and made arrangements to add copper, 1 part to 50 million, to the water in some of the beds. It worked exactly as Nägeli has described. The Spirogyra was destroyed without injury to the cress. The cost was negligible. This led to a further study in the use of copper in destroying algae of various kinds in water reservoirs. Certain forms of alga growth make water almost impossible to use at certain times of the year, due to bad taste and odor imparted to it. Methods were worked out making it possible by treatment with copper to remove any of these contaminating species at small expense. The methods developed have now become standard sanitary engineering practice.

The next development grew out of the observation that in these copper-treated waters certain species of bacteria were greatly reduced in numbers. These belonged to the *colon* group. Tests were therefore made on typhoid, para-colon, Asiatic cholera and related species. It was found that these could be destroyed in a few hours by the introduction of small amounts of copper sulfate or metallic copper without the slightest danger to those using the water. Certain types of fish, however, were killed. This led also to the testing of chlorine for these types of bacteria. Chlorine was found to be effective in destroying bacterial pollution without injury to fish but did not destroy algae. Both methods have now become standard practice in sanitary engineering.

The next development grew out of the observation that mosquito larvae were killed by these traces of copper, 1 part to 10 million. Colonel Gorgas requested that we send one of our men with him to clean up the zone in the Isthmus of Panama through which we were to dig the Panama Canal. The late Karl Kellerman was assigned to the job and used the copper treatment extensively in destroying algae and mosquito larvae when it was not practicable to use oil.

The use of copper in water supplies was followed by a study of copper in animal nutrition. The results of that study show that it is absolutely essential along with iron for haemoglobin formation in the redblooded animals. Its absence in the diet brings on secondary anemias that result in death if copper is not supplied. A trace of copper also proved to be essential in the growth of plants. What the next chapters will be I do not know. But I do know that Nägeli's work on "frog spittle" paved the way for work of very great value to humanity many years after he had passed away.

We must encourage and support research in all fields. It is the only key to progress. Botanical research has made it possible to produce food sufficient for earth's teeming millions if they will stop fighting and intelligently use the knowledge already gained.

In conclusion, I am sorry that the last annual report of the Brooklyn Botanic Garden did not come to my attention before I prepared my address for this evening. A discussion of that report would be a forceful presentation of botany and human affairs. The Brooklyn Garden is outstanding among the gardens of this country in its public relations contacts and in its cooperation with civic agencies of city, state and nation, in educating the public to appreciate the value, to the community, of botany in its many aspects and relations. Director Gager has been selected as chairman of the subcommittee having in charge this aspect of the plans for the National Botanic Garden at Washington.

TWENTY-FIVE YEARS OF CYTOLOGY, 1910–1935

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In the time here available it will be possible only to touch upon a few lines of study in which, or so it may seem to the writer, conspicuous progress has been made. For the sake of brevity, names will be used but sparingly at the risk of seeming to overlook many important contributions.

In the year that the Brooklyn Botanic Garden was established, it was announced that in seed plants chondriosomes, hitherto well known in animal cells but little studied in plants, become transformed into plastids. Through the studies so initiated, it has become clear that certain " chondriosomes " only develop according to the scheme of Pensa and Lewitsky, and that these are really the proplastids described many years earlier by Schimper and Meyer. Chondriosomes, speaking generally and including those of both plants and animals, are now recognized as a group of cytoplasmic inclusions marked by something of chemical likeness and therefore similar in their reactions to fixatives and dyes; but comprising bodies of distinct types differing in origin, function, and essential nature.

In addition to this heterogeneous class, and apart from structures peculiar to particular cells such as eggs, spermatids, and androcytes, the cytoplasm includes with greater or less regularity vacuoles, plastids in photosynthetic organisms, Golgi material in animals, and varied " ergastic " substances. Notable advances have included the development of methods of *intra vitam* staining; the elucidation of the nature of the vacuoles of meristematic cells; and the belated recognition of vacuoles in metazoan cells. Possible relations between classes of cytoplasmic inclusions are still under discussion; the Golgi material is variously held to be analogous with vacuoles, with vacuoles plus chondriosomes, with osmiophilic platelets, and even with plastids.

This cursory mention does not adequately suggest the difficulty of the study of cytoplasmic structure. Nor is it indicative of the thousands of pages that have been devoted to the subject. In no field, perhaps, has loquacity been more in evidence. It is pleasant to add that no imputation of over-expansiveness can be directed against American contributors. Faced by a happily increasing paucity of publication facilities, we are compelled, whatever our wishes, to spare our verbiage and our readers.

In a discussion of this nature in 1910, some emphasis would have been placed upon centrosomes and related structures. Not much more can be said now on this topic than might have been said then; partly because centrosomes early attracted an attention disproportionate to that devoted to other parts of the cell. Students of higher plants, who have done well without centrosomes for many years, may view with equanimity the discussion lately raging among zoologists anent the objective reality of these structures.

As to the cell wall, its constituent layers are being more sharply delimited; something has been learned regarding their finer structure; and progress is being made toward an understanding of the secretory processes leading to wall-deposition. Of particular interest in this field is the application of X-ray analysis to the molecular structure of cell-wall constituents.

More is to be said of the extension of knowledge regarding nuclear structures. Among these, nucleoli have long been most puzzling. Hypotheses concerning these have abounded in proportion to the scarcity of actual knowledge. At last a definite advance has been made in our conception, not yet of their nature and function, but of their origin and relations. The new views start with the observation by Navashin that in the prophases of mitosis the position of certain satellite-bearing chromosomes has a definite relation to that of the nucleolus; and with that of Heitz that nucleoli may arise in the telophases in close proximity to a satellite-bearing fiber or to an achromatic portion of a chromosome. Navashin's observations were incomplete, and Heitz' generalizations unduly sweeping. But it is established that very often, though not always, the position of a nascent nucleolus is related to that of a special part of a certain chromosome; and that often, though not always, the positional relation persists through the resting stages and into the succeeding prophases. The mystery of the nucleolus is far from solution; but a clue is at our disposal.

Of all cytological problems, it is that of the chromosomes which, as almost ever since Schneider's classical discoveries of 1873, still attracts most attention. At the beginning of the century, workers in the new field of genetics found in the chromosome theory an established mechanism ready to hand for the explanation of Mendelian and, as later appeared, of much non-Mendelian behavior. The newly emphasized importance of the chromosomes gave added impetus to their study.

Already by 1910 chromosome numbers had been determined for many plants and animals, although such lists as those published in 1915 and 1916 seem extremely modest compared with the formidable later compilations. The taxonomic importance of the series of chromosome numbers characterizing species of a genus and genera of a family was early emphasized. Cytological

observation and experiment have shown that from old races with fixed chromosome complements new races with differing complements may and often do arise. We find that such modifications result from disturbance of the orderly processes of mitosis and meiosis as well as from parthenogenesis, apogamy, and apospory; and that these deviations occur both in nature from unknown or at best suspected causes, and in culture in consequence of controlled manipulation. To what extent the new and deviant races may become established as reasonably constant varieties and species is still uncertain. Many of them are inconstant; others are incapable of competitive survival. But the heteroploid series which many genera present indicate that chromosome changes of the general nature of those observed must have played some part, probably an important one, in the origin of species.

Paralleling the study of chromosome numbers has been that of chromosome-form and -structure. In very early cytological studies size differences were recognized between certain members of the same genom; chromosomes as they moved toward the spindle poles were observed also to take on varied forms as of I's, J's, and V's. By 1910 it was recognized that constant and characteristic differences such as these are frequent enough to justify the hope that any given species may be described in terms of chromosome number, size, and form at least as fully and accurately as in terms of external characters. In very large measure that hope has been realized.

Its realization has been materially aided by the discovery of two special chromosomal characteristics: localized constrictions and satellites. The appearance of either of these peculiarities of structure varies apparently with nutritive conditions as well as with the stage of nuclear development. Certainly it varies with the method of fixation. What appears at times as a constriction seems at other times to be an achromatic region; but whatever its appearance it represents a permanent, definitely localized, and hence a diagnostic character. Very generally, if not universally, omitting from consideration telomitic chromosomes if such exist, a constriction or achromatic region is present at the point of spindle-fiber attachment. Additional constrictions (or achromatic regions) occur at other points in certain chromosomes. These too are definitely localized structural characters.

Satellites, first recognized by Navashin in *Galtonia,* are found also to be of frequent occurrence. While still too early to generalize, it is notable that in almost every angiosperm studied with reference to this point, with chromosomes large enough to be favorable for study, at least one pair of satellite chromosomes is found. In some instances a satellite seems to be lacking although there is a fiber (" seta ") at whose distal end a satellite might be expected to appear. If a satellite is present, the attaching fiber varies in

length in different cases; and it is quite possible that the appearance of a satellite is due to an extended and attenuated subterminal constriction.

Although the occurrence of constant morphological distinctions between the chromosomes of any race inevitably suggests the coexistence of functional differences, it was the discovery of chromosomal distinctions correlated with sexual characters which first made possible the assignment of a definite genetic function to a particular chromosome. Although sex chromosomes have been observed in insects for more than forty years, and their relation to sex in animals has been recognized for more than thirty, it was not until 1917 that such bodies were found in a plant. They are now known in about thirty dioecious bryophytes and about fifty dioecious angiosperms. The characteristics of the sex-chromosome complex vary from species to species among plants much as they do among animals. In most bryophytes possessing such a complex (omitting heteroploid strains), the female has one X, the male one Y. In most cases the X is the larger; but in two hepatics the Y is said to be larger than the X. In two *Frullanias,* the Y is reported as lacking, the female then having one more chromosome than the male. In dioecious angiosperms with sex chromosomes, most commonly the pistillate plant has two X's, the staminate an X and a Y. In certain species of *Rumex,* and apparently in one *Humulus,* the Y element consists of two chromosomes, the X of one; hence the staminate has one more chromosome than the pistillate plant. In one strawberry, the staminate plant seems to have two X's, the pistillate plant an X and a Y.

A characteristic of certain sex chromosomes now attracting some attention is "heteropycnosis." By this term is implied a tendency for the whole or part of a chromosome, most commonly the X, to remain condensed and hence deeply stainable at stages ranging from telophases through resting period and prophases, when other chromosomes are in a more diffused condition. The heteropycnosis of the X chromosome in certain insects once led to its designation as a "chromosome nucleolus." It is evident that there are degrees of heteropycnosis; that the intensity of the condition varies with the state of activity of the cell; that, while many sex chromosomes are at one time or another heteropycnotic, others are not; and that autosomes may display heteropycnosis. One writer, starting with the premise that heteropycnosis characterizes many sex chromosomes, has concluded that this condition, wherever seen, whether in allo- or in autosomes, is to be taken as evidence of the presence of genes concerned in sex-determination. The deduction supplies a beautiful illustration of the undistributed middle term.

Observations of another category concern visible internal chromosomal differentiations. These are mainly of two sorts: *chromomeres,* darkly staining

granules or discs, usually described as imbedded in a lightly stained or non-staining matrix; and spirally wound, darkly staining *chromonemata,* also at certain stages included within a lighter matrix. Although both types of structure were described early, chromomeres by Balbiani in 1876, chromonemata by Baranetzky in 1880, the orthodox account for many years was of chromomeres included in a slightly chromatic substance. The revival of the chromonema doctrine by Bonnevie in 1908 directed attention to the alternative conception. The present trend is toward the recognition of a spirally coiled chromonema constituting at certain stages the core, at other times the whole, of a chromosome. It remains to reconcile many well-authenticated observations of chromomeres with the widespread if not universal occurrence of chromonemata. Some appearances of distinct granules may be explained as incomplete or misinterpreted optical views of chromonemal coils; whereas those who hold to the reality of chromomeres explain chromonemata as continuous or apparently continuous chains of the smaller granules. It must not be overlooked that bodies of very different order have been referred to as " chromomeres "; for example, the large chromatic bodies, few in number, appearing as localized swellings on the chromosomes of *Phrynotettix.* Possibly analogous are the " knobs " borne by certain maize chromosomes. Whatever conclusion is finally reached regarding the nature or reality of chromomeres in general can hardly apply to structures of the nature and magnitude of these.

Mention must not be omitted of the momentarily modish objects of cytological study—the chromosomes of salivary-gland cells in flies. Here appears to be a detailed intimate structure on a relatively enormous scale. Descriptions of different observers, particularly when made on different species, are not yet in perfect agreement; nor is it possible to harmonize these descriptions with those of chromosomes in a more usual—perhaps more normal—condition. The usefulness of such giant chromosomes for purposes of genetic mapping, at least in *Drosophila,* is demonstrated; their cytological significance is a problem for the future. It is interesting that the classical figures most often copied as illustrating " chromomeres " are those old ones of Balbiani showing the " bands " or " rings " that mark the giant salivary-gland chromosomes of *Chironomus* larvae.

It is especially the study of chromonemata which has led to revised views of the process of mitosis. While the notions of the essentials of this process established more than fifty years ago have not been overthrown, our conception of the actual course of the process has been modified, and we hope clarified, by recent observations. Particularly does it appear that the longitudinally double nature of the chromosomes, long explained by a lengthwise

split during the prophases of the division in which the separation of the halves is to occur, really goes back at least to the later stages—very possibly to the prophases—of the previous division. We are more careful than of yore, too, in speaking of a *splitting* of chromosomes. The revival of Haeckel's old notion of perigenesis, combined with the modern idea of an autocatalytic power of living matter, promises an explanation less crudely mechanical than that of a simple splitting for the apparent doubling or quadrupling of chromosomes. It is the chromonema which gives a persistent entity to a chromosome; at certain stages this is enclosed in a matrix; at other stages the chromonema emerges, single, double, or quadruple, spiral or otherwise contorted or more or less straightened, as the whole of the chromosome.

A study of chromonemata has been involved, too, in the elucidation of some of the mysteries of meiosis. The controversy between parasynapsis and telosynapsis, still smoldering in 1910, is now a matter of ancient history. Parasynapsis is recognized as the mode by which pairing occurs in the heterotypic prophases—a pairing often prepared for by an approximation of homologous chromosomes much earlier in the life cycle. It seems clear, despite vigorous assertions to the contrary, that the last premeiotic division is in no essential different from an ordinary somatic division. As in any other somatic division so in this, each daughter chromosome, at least as early as the anaphases, contains two spirally coiled chromonemata. These persist through telophases and resting stage, reappearing closely appressed in the early heterotypic prophases. Then the double chromosomes pair closely, the two of a pair being often more or less twisted about each other. The matrices disappear. The chromonemata are now chromatids; each laterally approximated pair of chromosomes then includes four chromatids. In time the chromosomes of a pair separate somewhat, but now show interconnections which indicate that at certain points breaks and new connections have occurred, involving at each level, so far as has been demonstrated, only one chromatid of each chromosome. The occurrence of chiasmata so occasioned, cautiously suggested in 1909 by Janssens, has become an established fact. But the precise time of chiasma-formation, and the causal factors involved—these are still matters of speculation and hypothesis.

The recognition of chiasmata representing recombinations of parts of chromatids, together with a tendency to terminalization of chiasmata as the chromosomes contract and separate, help to a more adequate understanding than was previously possible of the later stages of meiosis and of its results in inheritance. They explain, of course, the genetic phenomena of crossing over; indeed, the necessity for such explanation furnished a major stimulus to the investigation of chiasmata. They supply, too, the significance of *two*

meiotic divisions, whereas it had seemed that chromosome reduction might adequately be effected by one. They explain how the four nuclei produced by the meiotic divisions may be qualitatively different—as has been shown experimentally to be the case in several fungi and in one hepatic.

Another line of study much younger than the twentieth century is that of the effects cytological and genetic which follow upon the transverse breaking of a chromosome. When, some thirty years ago, the possibility of an interchange of substance between laterally paired meiotic chromosomes was being suggested, the objection was sometimes made that such interchange would violate the law of the persistent individuality of chromosomes. The doctrine of individuality, brilliantly supported by Rabl and Boveri, still possesses much validity. But as a law it may be said to have been repealed. Nature cares little for the unit integrity of chromosomes; though we know not her methods of producing the same results, we can cause the breaking of chromosomes by bombarding them with protons, electrons, or photons. The study of the disturbing effects of radiation upon cytological processes is not a new one; it is of interest that the present Director of this Garden was studying the problem as far back as 1908. What is recent is some knowledge of the effects of chromosome-fragmentation upon specific chromosomes and of its genetic results.

A break or breaks having occurred, the fate of the fragments formed is various. One portion may be lost; very probably a fragment lacking a preexisting spindle-fiber attachment must disappear. A fragment may be reattached to its sister fragment in an inverted position; it may become attached to another chromosome; or, if breaks occur simultaneously in two chromosomes, fragments may be interchanged. One possible genetic consequence is reduced viability or absolute non-viability. Many chromosomal changes necessarily bring about modifications in linkage relations which may induce cross-sterility. Segmental interchange introduces greater or less intersterility between the parent form and that with the new chromosome-arrangement. Intersterility in turn leads to a degree of physiological isolation, enabling or encouraging the divergence of races and the formation of new species. Hence chromosome-fragmentation, like changes in chromosome number, would seem to have been an evolutionary factor.

One who has reached the conservative period of ontogeny may venture to regret a tendency, common to cytology and politics, to accept new conceptions because of their novelty. We are told, for example, in the true spirit of reform, that spindle fibers do not exist because they can not be seen in living cells, or in fixed cells after the use of a stain that is well known to stain nothing but chromosomes. There is ample room for a discussion of the

nature of spindle fibers. They may not be *fibers* at all, in the ordinary usage of the term. But that localized differentiations exist, in the form and position of what have been called spindle fibers, is one of the best-authenticated facts of cytology. Likewise unjustified are certain very modern views of the cell plate. Whether the droplets or granules that appear in the equatorial plane of the spindle are swellings of the spindle fibers or lie between them is a problem whose solution lies near the limits of microscopic possibility. The most careful studies, though no longer novel, have come to the former conclusion. The droplets swell and unite, so forming the cell plate. This plate does not become a wall layer; on the contrary, it splits and its halves become part of the bounding protoplasmic membranes of the daughter cells. These results are not to be discarded because some inexperienced person dabbling with such notoriously erratic fixatives as Benda's—useful for chondriosomes and for little else—is unable to corroborate them. The use of this fixative has led one author to conclude that polar caps—the form commonly assumed by the spindle rudiment in vegetative cells—arise within instead of outside the nucleus. His figures, taking them at full face value, are not demonstrative; and his conclusion is contrary to that reasonably based upon innumerable observations. Yet it has been seriously cited as overthrowing all that had gone before.

Results of a general bearing, such as most of those already mentioned, have come most largely, naturally enough, from studies on seed plants and on the higher metazoa. But questions peculiar to other phyla have by no means been neglected.

Referring only, and briefly, to certain of the so-called lower plants, material information has accrued regarding the details of syngamy and of gametogenesis, particularly of spermatogenesis, in pteridophytes and bryophytes.

In the algae, interest has centered in the determination of the time of chromosome reduction. In 1910, this was definitely known for two green algae, three browns, and two reds. It appeared probable that in all green algae, as in *Coleochaete* and *Spirogyra,* reduction is zygotic, the vegetative part of the history being haploid. Now it appears that all conceivable conditions in this respect occur in different greens: zygotic, gametic, and sporic reduction, the latter accompanying an alternation of generations. Without an exception thus far known, a cytological alternation of generations occurs in the browns and, save for one order, in the reds. In the exceptional order of reds, reduction is ,ygotic. As to the diatoms, long subject to question, gametic reduction seems to be established for both sub-classes.

It is less easy to generalize regarding fungi. In ascomycetes before 1910,

in basidiomycetes partly before and partly since, the time of reduction has been determined. Whether, and how, we are to speak of an alternation of generations depends upon definitions—and the fungi are little concerned with definitions. Despite the vast amount of cytological study devoted to them and the great mass of detailed information acquired, the minuteness of the structures involved and the awkward adherence of the fungi to an individualistic philosophy render almost any broad statement dangerous. Of all fungi, perhaps it is the rusts whose vagaries have afforded most entertainment. After scores of detailed investigations of their " sexuality," and after almost as many divergent conclusions, we seem at the moment to be returning to the thirty-year-old conception of the fusion of pairs of cells in the young aecidium. More assuredly than any other class of plants, the rusts promise endless material for future doctoral dissertations.

LIGHT ON VEGETATION, 1910–1935

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A tremendous band of energy left the star Arcturus in a single second in the year 1893. It fell away inversely as the square of the distance through which it travelled. Moving away with a speed of more than 186,000 miles each second this intense band of energy travelled an enormous distance in a single year. After 40 years it reached the earth. Both time and distance had taken a heavy toll and only an infinitesimal speck of energy was left. Meantime, man had toiled on during these 40 years. He had learned how to catch energy and how to multiply it until it could be made to perform a certain amount of work. He caught the speck of energy, added some more to it, and used this to open the Century of Progress Exposition where he might present the story of his achievements.

Today we are again assembled to take stock of human accomplishment in another field, the study of the effects of light on vegetation. Knowledge in this and other fields is not like the band of energy travelling out from the star Arcturus, ever falling away toward zero. Knowledge is cumulative and therefore operates in exactly the reverse order, each worker contributing an idea to that which has gone before. Progress at any time seems slow but when considered over a period of years many facts stand out as definite contributions to the ever-growing band of knowledge.

Thus the year 1893 already mentioned is an outstanding date in the progress of our knowledge of light on plants. This year saw the completion and final publication of Bailey's studies at Cornell (4, 5, 6) on the growth of plants under carbon arc lamps. This was the first detailed study of such a use of artificial light in America, although Siemens (20) had published the results of a brief study in England in 1880. Siemens observed that plants grown directly under the open arc lamp were seriously injured or killed. Placing the plants farther away, or even better, placing a glass globe around the arc greatly decreased the injury. Bailey also observed these facts but was convinced that with further study the injurious effects could be eliminated. He concluded that the electric light promotes assimilation, often hastens growth and maturity, and sometimes increases flower production. He stated further that plants need no rest at night in the sense in which animals need

rest, they can be grown in continuous illumination; "it is only necessary to overcome the difficulties, the chief of which are the injurious influences upon plants near the light, the too rapid hastening of maturity in some species, and in short, the whole series of practical adjustments of conditions to individual circumstances." Spinach and radishes tended to produce excessive top growth and had a tendency toward seed stock formation when lights were placed close to the plants and used for several hours each night as a supplement to daylight. Lettuce also produced a rapid top growth. This was more desirable in case of lettuce and spinach which are grown for the leaf crop, but objectionable in case of radish since the increased top growth restricted the development of the fleshy root.

The above observations were made almost two decades before the founding of the Brooklyn Botanic Garden in 1910 and are of interest in showing that even prior to our period of stock-taking a nucleus of knowledge had already formed about the subject matter. At the close of the next decade Garner and Allard of the Department of Agriculture published an outstanding contribution (7). They observed that Maryland Mammoth tobacco never produced seed in Maryland during the growing season but invariably produced seed when brought into the greenhouse in the fall even though the plants were cut back and only the root stumps planted. The soy bean had become quite a crop in the South. As early as 1908 Mooers (14) at the University of Tennessee had observed that certain varieties of soy beans always flowered at approximately the same date during the fall or late summer regardless of the time of planting. Garner, Allard, and Foubert (9) were interested in a study of the oil content as related to soil nutrients in soy beans grown in the greenhouse during the winter. They found however, that soy bean plants started to flower in winter before they had made anything like a normal growth. Temperatures in the greenhouse were essentially the same as summer so that this effect they believed, must be due to either light intensity or day length. By a series of carefully planned experiments Garner and Allard (7) showed that many plants which came into flower normally in the late summer or fall could be brought into flower at any time during the summer by shortening the daily light exposure period. This could be accomplished by placing the plants in a dark room at 4 p.m. each day and returning them to the daylight conditions at 9 a.m. on the following day. Shading with cotton cloth so as to reduce light intensity during the summer was not effective in bringing soy beans into flower. On the other hand such short day plants would flower during the short winter days with very little preliminary growth as seedlings. When these plants were illuminated with electric lamps for a few hours each night they were kept from flowering.

Garner and Allard found other plants which normally flowered during the long days of summer, such as lettuce and radish, which never flowered on the short winter days. These plants could be brought into flower by increasing the length of day by means of electric lamps applied each night. These were the long day plants. In Plate I *A* a typical series of short day plants, salvia, are shown which have been grown at the Institute with artificial light only on various day lengths ranging from 5 to 24 hours. Plate I *B* shows a similar series except that a long day plant, lettuce (Mignonette variety), was used. In addition certain plants like the buckwheat flowered on all day lengths, and these plants, Garner and Allard believed, correspond to the ever-blooming types which naturally occur in the tropics. They pointed out that the beet, which is a biennial in the latitude of Washington, often develops seed the first year when grown in Alaska. This they believed was an effect of the long arctic day and corresponded to the effect of the long day in forcing seed production in radish and lettuce which they had studied experimentally. They considered that day length quite generally was the determining factor in either biennial or annual habit of growth.

The last generalization beyond the facts which they had determined experimentally was later shown to be unsound by Thompson (22) and Miller (13) at Cornell University in 1929. They found that day length was not the factor which produced seed development in the two biennials, cabbage and celery, the first year, but a period of low temperature around 40° F. for 2 to 8 weeks was very effective. Later work by Thompson and Knott (23) indicates that even certain varieties of head lettuce can be brought into flower on a short day (10 to 12 hours) when the plants are grown at a high temperature. Later publication of day length effects by Garner and Allard (8, p. 892) indicated that the McCormick variety of potatoes yielded best on a comparatively short day length of about 13 hours. Many other plants produced larger underground storage organs on a short day and they concluded that such storage organ production was in general associated with a short day. Arthur, Guthrie, and Newell (2) working with the Irish Cobbler variety of potatoes found that at a cool temperature (68° F.) this variety produced the largest yields of tubers on the longest possible day even up to and including continuous illumination. Russian work (11, 16) and also that of Schick (19) indicates that many varieties of Russian and South American potatoes yield best on a comparatively short day. By way of summary, it is evident that either day length or temperature, or both may be effective in producing flowers and therefore seed formation in plants. It is certain that not all tuberization is brought about by short days. These effects may vary not only with species but with variety. It is therefore possible in some species to ob-

tain a variety which flowers only on a long day, another one which flowers only on a short day, while in other species and varieties temperature factors are more important than day length.

While plants can be grown under continuous artificial illumination, many varieties are greatly injured and in general most plants produce the maximum dry weight on approximately an 18-hour day (2). The Bonny Best tomato and the geranium are especially sensitive to continuous light. This may be due entirely to the quality of artificial light used. Tomatoes can be grown within the Arctic Circle on continuous sunlight. They can also be grown well in a combination of daylight supplemented by 6 hours of artificial light each night. The incandescent lamp is our common light source. Unfortunately, it has a ratio of approximately 90 per cent infra-red, or heat, to 10 per cent visible light as compared with an average ratio for sunlight of 55 per cent infra-red to 40 per cent visible light. It is known definitely that this light source is not as good in quality as sunlight as regards plant growth, yet when used as a supplement to sunlight for about 4 hours each night it produces very rapid growth and flowering in many varieties of plants.

A new type of greenhouse has recently been developed at the Boyce Thompson Institute in cooperation with the General Electric Co. to take advantage of these characteristics of the filament lamp. In this house the lamps are operated by means of a thermostat set to turn them on when the temperature has fallen to 62° F. Ten 500-watt lamps and the heat of sunlight constitute the sole sources of heat in the greenhouse. The house is built of sheet metal similar to a large refrigerator with a 6-inch layer of sawdust as the insulating material. An exterior view of the house is shown in Plate 1 *C*. Sunlight is admitted through a row of storm sash placed along the south face of the building. It was found that in practice the lamps never burned in the day time while the sun was shining even though the outside temperature was near zero. The lamps came on at frequent intervals during the night resulting in an average of about 4 hours of artificial light each night during the winter months. On cold cloudy days the lamps burned intermittently so that in practice light was supplied when the plants needed this most. Springtime growth and flowering of several species of plants were obtained in this house during the last winter at an average current consumption of 18 kilowatts per day for both light and heat.

This inventory of our knowledge of light on vegetation covering the last twenty-five years would nc be at all complete unless it included a discussion of the effects of quality or wave length of light upon plants. Both Siemens and Bailey had observed that the injurious effects of the carbon arc lamp could be practically eliminated by interposing a thin layer of glass between

the lamp and the plants. It has since been established that the injury is due to the high ultra-violet output of this lamp. Ultra-violet beyond the limit of sunlight, that is of wave length shorter than 290 mμ, is very injurious to plants (3). An exposure of 30 seconds to a mercury vapor lamp in quartz is sufficient to produce marked injury to young tomato plants. As more of the extreme ultra-violet is removed by means of appropriate filters, the time for producing the same injury increases rapidly until it requires more than 50 hours in one continuous exposure to produce any injury at a point just beyond the limit for sunlight. Meier (12) has recently shown that green algal cells can be killed by ultra-violet well within the extreme limit for sunlight (up to λ 302 mμ). While both the total ash and calcium and phosphorus fractions are increased slightly by exposing plants to these short wave lengths (21), plants grow well under ordinary glass which does not transmit this region and there is so far no conclusive evidence that plant growth is definitely benefited by it. Many of the red or anthocyanin pigments are produced or greatly increased in plant tissue exposed to the extreme ultra-violet region of sunlight. Poorly colored McIntosh apples (1) can be well colored by exposing them to a mercury vapor arc with Corex glass filters for a period of 3 days. This must be done as soon as the fruit is picked and placed in storage at a temperature of approximately 60° F. Cool temperatures and high ultra-violet are the essential factors for color production although a slight amount of pigment is produced even in the visible blue-violet region. Ultra-violet beyond the limit for sunlight injures the cells of the fruit so that they will not produce pigment. After the fruit is stored for a few weeks the epidermal cells lose their vitality and will develop no color. Color production here is a function of the living cells.

Schanz (18) in 1919 and Popp (15) in 1926 published studies of the growth of plants under colored glasses which absorbed various regions of sunlight. The studies showed that plants grew very tall and were pale in color when grown under the red region of sunlight. Under blue glass the plants were short but in general developed a darker green color. The poor development of plants under red glasses has been ascribed to the lack of blue light. It should be pointed out, however, that such glasses transmit the greater part of the infra-red while greatly decreasing the visible region. This results in a decreased ratio of visible to infra-red energy. Recently Johnston (10) has shown that the infra-red from a filament lamp produces pale leaves and that normal growth of the tomato plant can be obtained under continuous light when the infra-red is absorbed. It is apparent, therefore, that the infra-red has very definite effects on the growth and green color of plants.

Recent work at the Boyce Thompson Institute has shown that plants grown continuously under neon, sodium vapor, and mercury vapor lamps retain their green color but do not grow as tall as under the Mazda lamp. It is possible to add more red from a neon lamp to sunlight filtered through a red glass and produce a normal appearing plant; that is, by adding more red to the light which already contains only red plus infra-red, a more normal growth is produced. This in effect increases the proportion of visible red to the amount of infra-red. Conversely when a filtered band of red plus infra-red is added to the output of two neon tubes the usual elongation and poor color are produced which are characteristic of plants grown under the filament lamp.

Roodenburg (17) in 1930 found that plants grew well and developed good color under the neon lamp. He believed this was due to the location of the neon lines which correspond with the main absorption band of chlorophyl in the red end of the spectrum. Similar reasoning would indicate that the sodium vapor lamp would be of little value in plant growth since more than 95 per cent of the visible output of this lamp is in the single line at λ 588 mμ. On the other hand the mercury lamp should be a good light source since its main output corresponds closely with the absorption band of chlorophyl in the blue region. Tests made recently at the Institute indicate that the sodium lamp is the most efficient in producing dry weight, neon second, Mazda filament lamp third, and mercury least when calculated on an equal energy basis in the visible output of each lamp. In addition the sodium lamp is more than twice as efficient in lumens per watt as the incandescent filament lamp. Such lamps offer great promise in future work with plants as they have much less infra-red in proportion to the visible radiation and in addition the main output of visible light is found in the region where photosynthesis is carried on most efficiently. Further studies may show, however, that other bands of energy are necessary for complete plant development and must be added to the output of such a lamp.

While it is certain that in the future plants will be grown under artificial light with much less expenditure of energy, it is not reasonable to suppose that such light will ever compete with sunlight in practical plant production. From records of the New York Observatory for last December, it can be calculated that the average intensity of sunlight for the hour from 10 to 11 for the month was approximately 1900 foot candles. This is roughly the equivalent of the output of a 1000-watt filament lamp projected down upon an area 3×2.5 feet. It is at once apparent that such an amount of energy can not be disregarded. Practical considerations demand that sunlight be used during the day and that this be supplemented by the most efficient type of artificial light for the required number of hours each night.

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PLATE

A. A short day plant, salvia, grown on day lengths of 5, 7, 12, 17, 19, and 24 hours with artificial light.

B. A long day plant, lettuce (variety Mignonette), grown on various day lengths from 5 to 24 hours using artificial light only.

C. A new type of greenhouse, built similar to a refrigerator, heated and lighted by Mazda filament lamps.

Arthur—Light on Vegetation

TWENTY-FIVE YEARS OF GENETICS, 1910–1935

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In attempting to budget our discussion I find there is apportioned about one minute of talk for each year of research in our quarter century of genetics progress. I figure there were about 1000 geneticists who took part in the Fifth International Congress of Genetics at Berlin in 1927 and nearly as many were in attendance at the Ithaca Congress in the depression year 1932. A conservative estimate of the geneticists in the world during our period indicates that a pro rata distribution of time would allow 0.7 second to discuss one year's work of 25 geneticists or 25 years' work of a single geneticist. Seven tenths of a second is about the time necessary to pronounce the word "Genetics." You will appreciate my embarrassment, therefore, when I confess that my personal interest in genetics began about the year 1910, which is the starting point of our 25 year period under discussion. If I take more time to speak of the work with which my colleagues or I have been connected than would be necessary to say the word "genetics" it is only because it seems safer in such a large field to take my examples from work that is most familiar.

We often hear the expression "Leaders of Science." As a matter of fact so-called leaders often lead less than they are pushed. It is not the conspicuous spray which erodes the coast line of our continents but masses of water which surge forward with united front. We may change the figure and say that the advancement of science is like that of an amoeba—a mass movement with individual projections extending only a slight distance beyond the advancing edge. It is for this reason that so frequently important discoveries have been made independently at about the same time, as was the case with the rediscovery of Mendel's law. Mendel communicated his discoveries to Naegeli, an acknowledged leader in heredity and his published paper was cited in Focke's Cyclopedia of Hybridization in 1887. Some have thought that if Darwin had known of Mendel's work this important generalization would not have lain unnoticed for over 30 years. Darwin, however, made a cross between a peloric and a normal snapdragon (*Antirrhinum*) which gave a 3:1 ratio in the second generation without realizing the significance of this segregation. We are forced to conclude that Mendel was an offshoot so far

removed from the main body of thought of his time that he had no conspicuous influence in the advancement of biology, either then or now. It was the independent experiments of three investigators which led to the rediscovery of Mendelism in 1900 and it is the influence of 1900 which is felt today and not that of 1866 when Mendel announced his discoveries in the proceedings of the Naturforschender Verein of Brün.

The history of genetics may be divided into the ancient and the modern. The ancient history includes the early hybridizers from the time of Camerarius, 1690, to Darwin's " Origin of Species " in 1859 and the period that may be called the Age of Darwin from 1859 to 1900. This latter was an age of species and speculation. New ideas bring at first freedom but later bondage. And so the idea of evolution at first stimulated speculation but later stifled experimentation. The return to experimentation ushered in the modern period. This also may be divided into two parts. The period from 1900 to 1910 may be called " Mendelism and 3 : 1 Ratios " while the period from 1910 to the present may be labeled " Brass Tacks,—Genes and Chromosomes."

The early hybridizers were practically all botanists. I need mention only Camerarius, Koelreuter, Gärtner, Godron, Naudin and Darwin, who in experimental work would rank as a botanist. It was no accident that Mendel's law was first discovered through study of a plant, the garden pea, nor that this same law was independently discovered by three botanists, de Vries, Correns, and Tschermak, through their experiments with plants. Nineteen hundred was the birth year of modern genetics. Bateson became an early champion of the new science. He began his scientific life as a zoologist but largely reformed and became a botanist using plants as the chief objects of investigation and becoming director of the John Innes Horticultural Institution. The botanist, de Vries, early gave us the mutation theory and started a pack of botanical hounds on the eager trail after new forms of the Evening Primrose. A botanist, Johannsen, gave us the pure line theory—distinguishing what organisms appear to be (phenotypes) from what they actually are in hereditary constitution (genotypes). It is true that in this early modern period there were some zoological geneticists. The English school under the leadership of Bateson had worked on poultry as had also Davenport in this country. Cuénot in France had worked on mice and Castle had worked on rats and rabbits. Up to 1910, however, genetic investigations had been almost exclusively in the field of botany.

It was in 1910, or thereabouts, that the little yeast fly, *Drosophila*, was found to be an organism adapted to the study of mutations and Mendelian heredity, and a new era in genetics was inaugurated. The idea of using *Drosophila*, like most good ideas, had an evolution. An outline of this history

can be given from personal communications from Drs. Castle, Lutz, and Morgan. In 1900 Castle was looking around for material that could be bred in quantity for study of heredity in addition to rats, mice, and guinea pigs which he was then using. Professor C. W. Woodworth, an entomologist from the University of California, who was in Castle's laboratory raising *Drosophila* on fermenting grapes in a study of an embryological problem, suggested the availability of these little flies. After the season for Concord grapes was past, they tried other fruits and finally settled on bananas which remained the standard *Drosophila* medium for many years. It was later discovered that what the larvae really eat is the yeast and not the fruit and in consequence methods of cultivation have been greatly simplified. From 1900 to 1906 Castle and his students carried on experiments with *Drosophila* chiefly to discover the effects of continuous inbreeding. Around 1905 or '06 at the suggestion of Castle, W. J. Moenkhaus began to breed *Drosophila* in an attempt to alter the sex ratio genetically. Some of his work was carried on at Cold Spring Harbor. F. E. Lutz was working in Cold Spring Harbor at this time at the Station for Experimental Evolution of the Carnegie Institution of Washington and following the example of Moenkhaus took up the breeding of *Drosophila*. In the spring of 1907 he had under way a selection experiment on abnormal wing venation. A white-eyed *Drosophila* was found among some dead material, but this single variation was not further investigated due to the program of work on wing venation. A little later T. H. Morgan began looking around for available material for genetic work at Columbia where, very fortunately as it turned out, there were no funds for raising larger animals. Knowing of the other work on *Drosophila*, he tried out this animal which costs a laboratory so little for board and lodging, bringing in material from outside as well as getting cultures from Lutz. The science of genetics may be congratulated that the Columbia budget was meager in the days preceding our 25 year period, but the availability of *Drosophila* had already been established and other laboratories soon would have been using *Drosophila* in high pressure genetic studies if the Columbia laboratories had been wealthy and taken to breeding such an expensive and genetically undesirable animal as the elephant.

It may be of interest in this connection to mention a dozen organisms which have been used rather extensively as genetic reagents, listing them according to the number of gene types. Maize (our American corn) must be mentioned first with about 250 known genes. The snapdragon (*Antirrhinum*) is next with about 200 known genes followed by the Japanese morning glory (*Pharbitis Nil*) with about 110 and the garden pea with about 100. The sweet pea has about 20 known genes. In *Datura* we have about 40 genes

which have been located in the proper chromosome and about 200 or more others that we are calling genes but which we have not yet located. In animals we have in the domestic fowl, according to D. C. Warren, from 40 to 50 known genes. In the mouse there are around 25. In the rabbit, according to Castle, the identified genes number 16 located in 12 different chromosomes. In man, according to Davenport, it is safe to say there are not more than 25 to 50 genes that can be spoken of as known in the sense in which genes are said to be known in the other forms in our list. In *Drosophila melanogaster* there are 500 to 600 known genes not counting genes identified in several other species of *Drosophila*. In the parasitic wasp, *Habrobracon,* about 75 genes have been identified. Among plants, the Japanese morning glory is the only organism of much importance from the standpoint of the number of its known genes which had not been studied genetically before the beginning of our 25 year period. Among animals, the chief new organisms of genetic study are *Habrobracon* and certain species of *Drosophila*. *D. melanogaster,* as we have seen, had been studied considerably in the first part of our modern period. The difference between a good and a bad living reagent for genetic investigations may be seen by comparing man, the worst, with *Drosophila,* the best genetic " Versuchsthier," in respect only to rapidity of breeding (30 generations for *Drosophila* in a year) and the cost of cultivation. Proper techniques and proper living reagents are as important for research in biology as are techniques and reagents in research in physics and chemistry.

I have called the first decade of the present century the period of Mendelism and 3 : 1 ratios. This was a period of stock taking. Many characters had been found to Mendelize and give 3 : 1 ratios in the second generation, but it was still an open question how much of inheritance followed Mendel's law. Mendelian or " mosaic " inheritance was contrasted with blending inheritance. In a symposium on Botanic Gardens before the American Association for the Advancement of Science published in 1910 I spoke of plans to have both types of inheritance represented in the Agricultural Botanic Garden at the Connecticut State College. The Jimson Weed was used to illustrate mosaic inheritance but I remember having trouble in finding a good example of blending inheritance and East, whom I recollect consulting, could not help me out. The work since 1910 has changed the question so now we ask if there is any inheritance which is not Mendelian. Though some still claim there may be inheritance of a kind through the cytoplasm, the presumption is that if transmission from one generation to the next is not through the mechanism of genes and chromosomes, it is not to be called inheritance at all.

Since 1910 the field of genetic research has broadened both in respect to types of organisms and in respect to the structures and processes investigated.

Throughout the plant and animal kingdoms the method of inheritance has been found to be essentially the same, a fact which emphasizes the unity of living things. In the botanical field genetic study has been extended to the cryptogams. I need mention only the work of Dodge on the fungus *Neurospora* and that of Allen on liverworts. Mosses and ferns and even the smuts also can now be used to illustrate Mendel's law.

Genes have been identified which affect practically all parts and processes of the plant from early embryo to late fruit. Resistance and susceptibility to disease, the pH of the cell sap, the size of chromosomes, the self sterility of flowers have all been shown to be conditioned by known genes. In *Datura,* for example, we have found a gene responsible for failure of chromosomes to pair at reduction, the behavior of which has been worked out by Dr. Bergner; a gene which Miss Satin has investigated causes doubling of chromosomes; several genes responsible for abortion of pollen grains at different stages of development studied by Cartledge; and several genes also for abnormalities in pollen-tube behavior disclosed by the studies of Buchholz. Sinnott has shown that a single gene may cause profound changes in the anatomical structure both internal and external and Avery and the speaker have located genes which have such diverse effects as production of male sterility, reduction in size of flower, complete elimination of purple pigment or its restriction to parts of stem below the cotyledons and various defects in chlorophyll production. We may classify the different types of genes according to their method of action rather than according to the specific part or process which they affect. Thus we speak of complementary, multiple, duplicate, modifying, quantitative, and lethal factors. Genes may be trivial or important in their effects upon the organism. Naturally the geneticist who wishes characters as markers with which to follow the behavior of chromosomes in which their genes are located prefers those characters like floral colors which least disturb the life of the organism. It can no longer be said, however, that Mendelism has to do only with unimportant characters.

Timoféeff-Ressovsky has made a tabulation of genes according to their effect upon the viability of *Drosophila.* To every gene causing a visible effect he finds there are four genes that are lethal, that is which kill the organism, and ten genes which are sublethal, that is which reduce slightly the viability without killing the organism and with only a slight, if any, visible effect. Mutations with slight visible effects are most numerous. We seem thus to be getting back to Darwin's small fluctuating variations except that now we distinguish genetic from environmental causes of variation.

In the early days of genetics, we used to speak of unit characters as if each adult characteristic were caused by a single unit factor. We still speak

of unit factors but no longer of unit characters. We now realize that there is an interaction of factors with each factor influencing more or less strongly the expression of all other factors. It has been shown, for example, that for the normal development of chlorophyll in maize the interaction of at least 65 factors is necessary. We now speak of chromosomal balance and of genic balance.

Our quarter century, 1910–1935, I have labeled "Brass Tacks,—Genes and Chromosomes" because it has been during this period we have come to realize that it is possible to get down to brass tacks in genetics and that these brass tacks are the genes and chromosomes. In 1906 at the British Association for Advancement of Science I heard a symposium on what, if any, relation there is between heredity and chromosomes. The relation is now recognized as a simple one,—that of cause and effect. Bateson, who was such a valiant crusader and effective defender of the faith in Mendelism during the first decade of our century when the new teachings were attacked by biometrical opponents, never fully accepted chromosomes as a mechanism of heredity. At the Toronto meeting of the American Association for the Advancement of Science in 1921, he made public confession of his conversion to belief in chromosomes, but he never came to think in terms of chromosome behavior.

It will be possible to outline only some of the more important new principles established in the last 25 years. In doing so it will be noted that these discoveries must be described in terms of chromosomes and their constituent genes.

First may be mentioned linkage and the linear order of the genes established in *Drosophila* through crossing-over values. It is true that Bateson and Punnett had earlier discovered linkage and breaks in linkage in the sweet pea, but they had called this coupling and repulsion and had explained the phenomenon by an hypothesis of differential rates of division of cells preceding the formation of gametes.

An important discovery in the latter part of our period was that like parts of chromosomes are together at reduction and that the attachments of known chromosomes may be used to identify the ends of unknown chromosomes. Belling used this method effectively in interpreting heteroploid types in *Datura* and with it worked out the important discovery of segmental interchange which is a process of chromosomal rearrangement not uncommon in nature. Simple translocations in which a part of a chromosome has become permanently joined to a non-homologous chromosome had been discovered in *Drosophila* in the earlier part of our period.

The study of heteroploidy is a development chiefly of the last 25 years. It is true that heteroploidy of different kinds was found in *Oenothera* before our

period began but the tendency was to consider the extra chromosomes as a characteristic rather than as a cause of the mutant types in this genus. The mutations in *Oenothera* responsible for " elementary species " were thought by de Vries and his immediate followers to involve the formation of new hereditary units. We now classify them not as gene but as chromosomal mutations and explain their effects as due to a change in chromosomal balance. At one time *Oenothera* appeared to be an anomalous genus in its hereditary behavior with little bearing on the genetics of other groups. Due to three major discoveries made within our period,—Muller's balanced lethals, Cleland's association of chromosomes in circles, and Belling's segmental interchange, the breeding behavior in *Oenothera* is becoming better understood and other forms are being found to exhibit similar phenomena.

Unfortunately time will not permit a further discussion of heteroploidy which is a subject of more importance in Botany than in Zoology. I should like to point out the value of $2n + 1$ types in an analysis of the factorial constitution of unaltered chromosomes and the use of trisomic ratios in locating genes in maize as well as in *Datura*. Search for information about chromosomes has led to investigation of their intimate behavior in the early thin thread stages. For example, valuable information has been obtained in maize, notably by McClintock, regarding the pairing of chromosomes in these early stages. What actually happens at the time of crossing over in the chromatids and the function of chiasmata is still a question debated by Darlington, Sax, and others.

The search is being extended to still further recesses of the chromosomes and investigators such as Demerec are studying the very nature of the gene itself which was once considered only an imaginary concept like the equator which we may sail over in the tropics without feeling any bump.

Among the important advances in the last 25 years should be mentioned three techniques. The aceto-carmine method holds among techniques the position that *Drosophila* holds among " Versuchsthiere." It has enabled studies to be carried on with large numbers that would not have been possible with sectioned material. Belling's contribution to the technique was the addition of iron which left the cytoplasm clear. Other modifications have been made by different investigators but he was the first who used it extensively in cytogenetic work.

The second technique to be mentioned is the induction of mutations by radiation treatment. The chief credit for this discovery properly belongs to Muller but like most discoveries there is considerable history back of it. The desire to control the type of offspring is earlier than modern genetics. You remember the account in Genesis, dated B.C. 1747 in biblical terminology,

which described Jacob's method of increasing the proportion of spotted lambs, which were his share of his father-in-law's flock, by exposing peeled rods before the ewes at time of mating. More nearly in our present period is the suggestion made by de Vries in an address in 1904 at the dedication of the Station for Experimental Evolution. He urged that the rays of Roentgen and Curie, which are able to penetrate into the interior of living cells, be used in an attempt to alter the hereditary particles in the germ cells.

In the beginning of our period Loeb and Bancroft, with the assistance of Bagg, used x-rays, radium, and high temperatures in an attempt to induce mutations in *Drosophila*. Some mutants were obtained but there is no clear evidence that they were not already in the stock when the treatments were started. It is also probable that the mutants later obtained in mice by Little and Bagg, some generations after treatment with x-rays, were homozygous extractives of genes already present in the stock. Morgan early carried on some work in treating *Drosophila* with radium, with the result that some of the descendants of the treated flies produced mutants of the ordinary type. The work was not followed up apparently because the numbers of mutants were small and the effects not specific. Mavor later obtained definite effects of radiation upon crossing-over and non-disjunction, and Gager, in cooperation with the speaker, in a single experiment with radium emanation obtained an increase in non-disjunctional types and a couple of recessives out of a number so small as not to be surely significant statistically. After Muller had announced the results of his well planned experiments it was discovered that both Stadler and Goodspeed had radiation experiments under way which later gave them an abundance of induced mutations. I need only mention here the induction of mutations by heat treatment, in which Muller also led the way, and the very recent discovery by Navashin, which has been energetically followed up by Cartledge, that merely aging seeds on laboratory shelf will increase their mutation rate. The ability to obtain at will an abundance of both chromosomal and gene mutations has been of tremendous value to experimental genetics and has made it possible to subject the process of mutation itself to experimental study.

The third technique of which it seems desirable to speak is so new that it is difficult to appraise its full value. The discovery that the structures in salivary glands of the larvae of flies are in fact chromosomes with markings corresponding to the gene loci appears to have almost staggering possibilities in the way of permitting an accurate analysis of chromosomal structure hitherto impossible. Imagine for a moment an astronomer who has been studying the planet Mars and trying by enlarging the telescopic lens and increasing the sensitivity of the emulsion on the photographic plate to learn

more of the structure of this heavenly body. He may feel that he has about reached the limits of increased vision by changes in telescope and photographic plate but in his wildest dream he probably never imagined he could induce the planet itself to grow bigger so it could be seen more clearly. This, however, is just the kind of a thing that has happened to the salivary chromosomes. They have swollen up not two or three times the usual size we are accustomed to but 100 and 150 and even 170 times the size of chromosomes in other parts of the fly. All the markings, which are being found to have so much significance, have swelled up from invisibility into visibility so that we can now count and chart them and determine their relation to our ultimate units, the genes. This like most other discoveries also has a history. Painter appears to be the one to be credited with realizing that the salivary structures were chromosomes with markings capable of being related to genes. Heitz independently, and in fact earlier, pointed out that the banding in the salivary chromosomes is a constant characteristic. Many others, some even in genetic laboratories, had figured them without sensing their significance in genetic research. Bridges and Koltzoff independently interpreted the salivary chromosomes as compound structures, consisting of two cables of many chromosomal strands. Bridges has given detailed drawings of the four salivary chromosomes of *Drosophila melanogaster* with a reference system for their markings which is being used by many workers in this new field.

It is interesting to note to what extent the study of evolution was restricted by the experimental work in genetics. It is only within the last few years that the methods used in genetics have been actively applied in an attack on evolutionary problems. Bateson in his Toronto address in 1921 despaired of genetics being able to offer any help toward a solution of the species problem. At that time, however, English botanists had already made discoveries in the behavior of chromosomes of *Primula Kewensis* which offered a clue to a method of species formation. In study of the species problem more progress has been made with plants than with animals. The differences between species have been studied by means of an examination of chromosomes of hybrids in *Oenothera, Viola, Crepis, Nicotiana, Datura,* and other genera. The conclusion is being reached that the problem of evolution of species may most profitably be investigated in terms of the evolution of their chromosomes. It is seen that blocks of chromosomal material with their genes can be readily shifted from one chromosome to another. Many of us have felt the inadequacy in accounting for the origin of new species by the mutation of single genes one at a time and have looked rather for differences involving whole blocks of genes. It was with considerable satisfaction, therefore, that we learned that the salivary chromosomes in *Drosophila* show reduplicated areas

in the chromosomes and thus give support to the idea of evolution by change in chromosomal balance. Experiments in the greenhouse and garden have given clues to what is found in nature. In the sterile hybrid form of *Primula Kewensis,* the chromosomes from the two parents, *P. floribunda* and *P. verticillata,* are unlike and hence have difficulty in pairing with each other in reduction divisions. When doubling of all the chromosomes of the sterile hybrid had taken place to form the "amphidiploid" fertile *P. Kewensis,* the chromosomes derived from each of the parent species had homologues with which they paired and a new pure-breeding species with a new balance was developed. Many other examples of the origin of amphidiploids under controlled conditions could be given and pure-breeding new types have been synthesized in *Datura* by addition of blocks of extra chromosomal material. By proper breeding manipulation of the chromosomes Müntzing appears to have duplicated a species, *Galeopsis Tetrahit,* found in nature.

In the early days of Mendelism much was heard of the presence and absence hypothesis which taught that the dominant character is represented by the presence of something material, whereas its allelomorphic recessive is due to the loss of this dominant gene. The presence and absence hypothesis has been abandoned as an explanation of genes in general but it is interesting to note that in *Drosophila* and maize detailed study of chromosomes in connection with breeding behavior has demonstrated that sometimes genes may be lost without lethal effect and in such cases the loss may behave like a recessive. It is not always easy to distinguish effects due to genes from those due to chromosomal abnormalities. In *Datura* for example, we have many cases in which blocks of extra chromosomal material behave like dominant genes in inheritance and we have at least one case in which the chromosomal block behaves like a recessive gene in that the heterozygous types are indistinguishable from normals although the homozygotes are readily recognized. The presence and absence hypothesis led Bateson to conclude that evolution must be a loss phenomenon, that man, for example, differs from amoeba in the large number of amoeba genes which man has lost.

Lotsy appears not to have worried greatly about the origin of genes in his attempts to explain all evolution by hybridization. Modern genetics is unable to support Lotsy's extreme views but it is becoming evident that, in plants at least, hybridization in connection with polyploidy has been an important method of evolution. In this connection I need mention only such forms as cultivated wheats in which the chromosome numbers ($n = 7$, 14, and 21) form an arithmetical series and in which evidence is at hand that the types with 21 pairs of chromosomes have a compound chromosomal complement made up of three different groups of chromosomes. Genera such as *Crepis,*

Carex, and *Drosophila,* in which the chromosome numbers of different species run more or less consecutively, afford evidence of evolution through major chromosomal changes rather than merely by means of the accumulation of single gene mutations. Polyploidy alone seems not to have played a great role in species formation in nature, though a number of true tetraploids (i.e., with 4 of each kind of chromosome) exist in the wild as distinct species or races. Among these may be mentioned the 4n species of *Empetrum hermaphroditum* apparently derived from *E. nigrum,* the 4n form of *Tripsacum dactyloides,* and perennial teosinte (*Euchlaena*).

The discoveries in genetics of the last 25 years have changed our viewpoints and through them altered our philosophy of life. I have touched on these matters elsewhere. I need only point out in this connection that a mechanism of heredity has been firmly established and as a consequence certain old problems no longer bother us. We do not believe in telegony, maternal impressions and the inheritance of acquired characters because they go counter to the established mechanisms. Before the mechanisms were known, they seemed reasonable. No geneticist now thinks of any conflict between belief in heredity and belief in environment since he is accustomed to take into consideration the responses of a given gene in different environments, not excluding the internal environments brought about by the interaction of other genes. Perhaps before telling of the wonders of genetics, geneticists can do a service to their own science as well as to their lay friends, who are inclined to take the side of environment as opposed to heredity, by pointing out that life cannot exist without both the proper heredity and the proper environment.

We have said that genetics narrowed the point of view of the student of evolution. Genetics has also had a broadening influence. A geneticist can no longer be a botanist or a zoologist only, since the laws of heredity do not recognize the classification into plants and animals. The subject has an integrating influence relating such subjects as physiology, cytology, anatomy, and taxonomy—in fact all the biological -ologies and -onomies. Its relation to experimental taxonomy is of particular interest since both are concerned with the study of evolution. I need only mention here the work initiated by the late Harvey Hall and still being actively prosecuted in California by the Carnegie Institution's Division of Plant Biology. Turesson's concept of Ecotypes (that the environment moulds forms by selecting out of a highly heterozygous population those genes of most value in the given environment) corrects Bonnier's idea of the direct effect of the environment upon habitat forms and shows how genetics and the experimental method may be of aid to taxonomy.

And now let us take two glances into the future.

1. Our last 25 years have brought us again to the species problem. I believe the study of evolution will become increasingly active. It will differ from Darwin's time in that it will be experimental and analytical. It will resolve itself into a study of the evolution of the brass tacks of genetics—genes and chromosomes.

2. When we have learned the mechanisms of evolution, I believe we shall be able, in ways and to an extent impossible to imagine at the present time, to exercise conscious control of evolution.

TWENTY-FIVE YEARS OF ECOLOGY, 1910–1935

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A quarter of a century is a long time when we look forward to it, and all too soon we reach the period when we fear we can not look so far ahead, but as we look backward through the nineteen-thirties and the nineteen-twenties to nineteen-ten, it seems much shorter. Nevertheless, the period has been long enough to have witnessed, not the birth, but certainly the development of two great branches of plant science, genetics and ecology.

No field of plant science can show a type of development which may be compared with the advances in physics and mathematics. There important discoveries may be made suddenly. There the mathematician can set up his rigid equations and with inexorable accuracy push them to their ultimate conclusions. The astronomer studies the stars in his office as much as in his observatory. The physicist writes with confidence about the electrons and protons which he has never seen.

But we biologists carry on our research with materials which have never been reduced to equations, which still require the continued use of the microscope, the laboratory, the garden, and the field; which often must wait for the completion of the work of the physicist and the chemist, and which are in general the most obstinate, the most refractory, the most baffling of all possible objects of study. These are living cells, living animals, and living plants. We must hurry with our work, for further progress in agriculture, in medicine, and even in sociology and politics is depending on us.

We do not need to search for the ultimate roots of plant ecology. They are many, and extend back for more than a century. In the United States, ecology began at the end of the last century. A promising young geologist and geographer, Henry Chandler Cowles, studied sand dunes, saw that they were as much the product of plant activity as of wind, and as a result became one of the foremost ecologists of our time. Roscoe Pound, a brilliant young lawyer, and Frederic E. Clements, an enterprising classicist, inspired by that master teacher of botany, Charles E. Bessey, studied the plant life of Nebraska, and became equally prominent ecologists.

Attracted by the novelty of their results and doubtless influenced also by the apparent ease with which results could be obtained, a host of others

undertook ecological investigations, mostly by purely observational methods. Throughout the country, young ecologists, of whom I was one, descended on the dunes, the shores, the marshes, and the bogs and presently returned to the laboratories to write voluminous accounts of their observations. By 1910, when the Brooklyn Botanic Garden was established, there was in existence a large body of ecological literature, describing in detail, but without much correlation or coordination, the general features of vegetation in most parts of the civilized world; certain fundamental ecological concepts had been firmly established, such as association and succession, and a few experimental methods had been devised.

All of these features have been further expanded and developed during a quarter of a century, and in addition certain other phases of the science have been added which promise to be of even greater value, not only as extensions of our fund of knowledge, but also as tools for the use of other disciplines of biology.

We assume that we, as individuals, reach our maturity and put away childish things, at the age of twenty-one. Plant ecology may be considered to have attained its majority when it first received serious consideration from an International Botanical Congress. The exact date of this event is May 20, 1910, almost precisely twenty-five years ago. On that memorable occasion at the Congress at Brussels, the veteran European ecologists Flahault and Schroter presented and recommended the adoption of certain definitions of ecological concepts, as a step toward the proper coordination of scattered ecological knowledge. We can only regret that the coordination which they desired is still not achieved.

The change in the viewpoint of ecology during the quarter-century has been striking. No longer is the mere superficial description of a piece of natural vegetation considered real ecological research. Instead, attention has been largely directed toward the discovery of the fundamental underlying principles which govern and control all phenomena of the living plant in its normal environment and toward the application of these principles to several economic problems and to other broader questions of pure botany.

One of the earlier developments in the science was the realization that ecology is extraordinarily polymorphic. Originally defined as the relation of the plant to its environment, it soon became apparent that the relation of the individual plant is an entirely different matter from the mass relation of numerous plants. The former, that of the individual, is manifested in the form and structure of th plant, and in the nature and the rate of its physiological activities. The study of the ecology of the individual is the study of its morphology and its physiology, carried on under natural conditions rather

than under the artificial or controlled conditions of the laboratory and always with the attempt to correlate the structure and the behavior with the environment. We believe that the results of such studies on one individual are applicable to all other individuals of the same race.

On the other hand, numerous plants, probably of many different races and with different structure and behavior, live together in nature and constitute en masse what we call vegetation. The structure and the behavior of vegetation offer an entirely different field for study, a field which differs from morphology and physiology as greatly as sociology differs from human anatomy. The great development of plant sociology has been one of the chief features of the progress of ecology during the past quarter-century.

Notwithstanding the differences between the two branches of ecology, it must still be clear that they are intimately connected, since the part which the individuals of any race play in vegetation depends on the success with which they can carry on their life processes; that is, it depends on their physiology.

During the past quarter-century, these two fields of ecology have continued to drift steadily apart. Today, such important investigations of individual ecology as the study of xerophytism and the ecology of crop plants are carried on largely by physiologists, and a majority of those botanists who style themselves ecologists are interested primarily in the complicated problems of plant sociology. It is interesting to note that, in the so-called Chicago textbook of about twenty-five years ago, ecology was presented almost wholly from the standpoint of the individual plant, while the recent text of Braun-Blanquet considers plant sociology almost exclusively.

It has long been known that natural vegetation is generally divided into definite areas, each of them uniform, or essentially so, in appearance and structure throughout its entire extent, and all of them separated from each other by fairly narrow transition zones. In any one limited region, the number of distinct kinds of associations may approach a hundred, while the number of distinct areas, each representing one or another of these kinds of vegetation, may naturally be very great. It is also evident that certain of these associations resemble each other rather closely and differ markedly from the remainder. The existence of these societies has led ecologists to produce a terminology by which they may be expressively described and a nomenclature by which they may be known and distinguished. They have also tried to classify these societies into groups of higher or lower degree, depending on their resemblances.

Exactly the same problems face the taxonomist, who finds the same series of difficulties in his work with species. What is a species? What is a genus? What are the evidences of relationship between them? Do the pines consti-

tute one genus, because of the similarity in their needles, or several genera, because of the differences in their cones? If, after nearly two hundred years of intensive work, taxonomists have not been able to agree fully on such questions, we should scarcely expect that ecologists should have succeeded in twenty-five years.

Nevertheless, progress has been made. We are at least able to describe a plant society with reasonable precision, and to compare or to contrast two societies of different regions. Our nomenclature is by no means as complicated as in taxonomy, and the confusion which is sometimes manifest is often as much philological as biological.

Concerning the nature of the association itself, two extreme views have been offered. The first of these holds that the association is a complex organism, the second that it is merely a fortuitous juxtaposition of plant individuals. Although the first view, in its extreme form, was generally rejected by ecologists, it is noteworthy that at least two keen students have recently defended the concept, but tempered it somewhat by describing the association as a quasi-organism, endowed with a number of functions peculiar to itself and not appertaining to any of the individual plants which compose it.

The contrasting view explains the association as the result of environmental selection from fortuitous immigrants; explains the repetition of similar associations in different places by the similarity in their environment and in the flora from which their population may be chosen, and denies the existence of any functions of the association beyond the sum of the functions of the individual plants. Although received with skepticism by many ecologists, and although branded as iconoclastic by the latest proponent of the quasi-organism theory, it is noteworthy that the most discerning critic among European ecologists has recently accepted this view almost in entirety.

There seems to be no middle ground between these two concepts, nor has any other reasonable idea been proposed. Although we have not succeeded during our quarter-century of progress in reaching a generally accepted idea of the true nature of the association, we at least have two concepts instead of none, and we have no doubt that another twenty-five years will see one or the other regularly accepted.

Whatever may be the true nature of the association, it is clear that two factors at least are intimately concerned, the physical environment, which decides what kinds of plants may exist in it, and the living plants themselves, which tend to control and to modify the physical environment. It is probable that every species of plant, no matter whether its individuals are large or small, abundant or few, reacts on its environment in a manner peculiar to itself, the so-called dynamogenetic behavior of the species. It also seems

probable that the joint reaction of the whole population is one of the most important factors in maintaining the uniformity and the equilibrium, and therefore the identity of the association.

One of the most interesting features of the relation of associations to each other is the phenomenon of succession. First brought into prominence by the work of Cowles, its study constituted a considerable part of ecological research twenty-five years ago. It was often considered that succession proceeded regularly in a predetermined direction and through a uniform sequence, culminating finally in the climatic climax, an association of great extent and permanence. So important has succession seemed to some ecologists that it was chosen by Clements as the fundamental basis of his classification of associations. According to his system, all the numerous associations which precede the climax are regarded as subordinate to it and as representing, so to speak, its juvenile stages. Such a system envisages the ultimate occupation of the whole land surface of the earth by a series of such stable, long continuing, climax associations.

There is no longer any doubt that succession between associations actually takes place, or that its causes are exceedingly varied. There is no doubt that some associations are stable and others unstable, that some are comparatively ephemeral while others endure for periods longer than we care to estimate. But the existence of a climax in permanently stable equilibrium is quite a different matter. It seems more probable, according to the keenly logical deductions of Cooper, that succession is a continuous, never-ending process, that successional series, instead of representing stages in the genesis of the climax, are merely evidence of a more rapidly changing environment, and that the fundamental feature of all vegetation is, as so tersely expressed by Cooper, the universality of change.

With thousands of different types of associations known to ecologists, the need of classifying them into superior groups is evident and various authors have proposed methods for it. According to Clements and some others, associations should be classified according to their history or chronology, and all those which normally follow each other in a successional series placed together, without regard to their structure or appearance. According to Rübel, associations should be grouped according to the vegetative form of their component species, without regard to their history or to the species which compose them. Classification, as is well known, is the process of grouping objects according to their similarity. Systematic botany has always chosen genetic relationship as the similarity to be used. Such a feature is not available in ecology, and we can only report with regret that a quarter-century of effort has brought forth no logical and generally acceptable system of classification.

For many years the description of vegetation was purely qualitative and often subjective in nature. A species was described as common or rare, a forest as dense or open, in terms which are purely relative or subjective, impossible of exact definition, and incapable of conveying a clear idea to a reader. The first crude attempts at remedying this condition by the quantitative expression of vegetational conditions were made just prior to our quarter-century, but all the real development has taken place since that time.

It is completely out of the question for an ecologist to make a detailed study of all the individuals comprising a good-sized piece of vegetation, since their number mounts up into the millions. As a substitute, the now well-known quadrat method was introduced and largely developed by Clements. It consists in segregating for detailed study a very small piece of the whole, usually only a few feet square, and technically known as a quadrat. On such a plot all the individual plants can be listed, counted, measured, mapped, and photographed. The results thereby acquired, however, are valuable only to the degree that the quadrat represents the average condition of the vegetation. Now the average quadrat is just as elusive as the average man. We can not picture the average man unless we first make a detailed study of the whole population, and from this study deduce our average. Similarly, we can not successfully choose an average quadrat except after a preliminary study of the whole.

We have found, fortunately, that the process can be reversed. Many carefully planned series of observations have shown that, within the extent of a single plant society, the individual plants and the various species of plants are distributed at random, or in other words, by chance. Therefore, a series of small quadrats, distributed at random over the area under study, will be sufficient to give us a clear idea of the average, and from a knowledge of the average we can arrive at a satisfactory idea of the whole. Then, if we wish, we can select for more intensive study one or more quadrats which will fairly represent the average of the whole plant society.

The first result of such statistical studies was the now well known frequency index, first introduced by Raunkiaer but developed largely in this country, where the basic equation was first formulated. By the proper use of this equation it is possible to determine, for any plant association, the number of individuals of every species without counting them. It also enables us to express by an intelligible index figure the relative importance of any species within the association, the constancy with which a species appears in scattered societies of the same general type, and the fidelity, or degree of exclusiveness, with which a species appears in that sort of vegetation alone.

Several practical applications of the frequency index have already appeared and probably others will be found in the future, such as the determination of

the importance of weeds in cultivated fields, or the detection of the deterioration of pasture land.

The problem of quantitative methods soon became one of the application of mathematical laws to ecological observation, and introduced questions which even our most skilled mathematicians are apparently unable to answer. For example, two attempts have been made by empirical methods to develop an equation by which the number of species in an area can be determined without the labor of a careful census. The two equations are radically different and one of them obviously leads to incorrect results if used on too large an area; nevertheless neither of them has been completely proved or disproved by mathematical analysis.

Some other mathematical concepts have been developed and later found to be useless, and at least one has proved to be merely a complicated way of stating an axiomatic fact. The general value of quantitative methods has been so thoroughly shown, however, that we may predict a still greater development during the quarter-century which lies before us.

The essential facts of the geographical distribution of plants were known long before 1910. For more than a century also, explanations of this distribution had been offered, most of them seeking to account for observed facts by temperature or rainfall. Fifty years ago Engler introduced the idea that modern distribution is a matter of history and can only be accounted for by the distribution of plants in the past. Numerous observations also indicated very clearly that there had been great migrations of plants in the past. Studies of succession showed something of the details by which these migrations had been accomplished and led to the inference that they were still in progress.

Unfortunately no means were available for determining what these migrations had been except the very incomplete evidence of fossils and the present existence of relict colonies. Nor was it always possible to distinguish between a pioneer and a relict colony, until study of succession showed that pioneers advance in the territory best suited to them, while relicts linger behind in territory least suited to the immigrants. By the use of these crude tools alone, considerable progress was made in tracing out the past migrations of plants and thereby in reaching a reasonable explanation of their present geographical distribution.

A new and far more powerful means was brought into service in 1916, when Post showed that fossil pollen was abundantly preserved in bogs and that by a careful quantitative study of it we could trace out past migrations of plants and discover past changes of climate with far greater detail and precision. Although first utilized in Europe, it has recently been introduced into America, with equally striking results. The pollen in successive layers of a

post-glacial peatbog gives a general picture of the prevailing vegetation of that neighborhood from the first formation of the bog to the present time. Even the direction of plant migration may be shown. If contemporaneous strata of peat in two different bogs show pollen of beech, for example, only in the western bog, and if beech-pollen appears in later strata of the eastern bog, it is clear that post-glacial migration of the beech proceeded from west to east. In this way the Europeans have built up a remarkably comprehensive picture of the whole history of vegetation in western Europe since the ice-age.

In America our results are not so complete, since the amount of data available is not yet sufficient to permit extensive generalizations. Nevertheless, some striking results have been reached. From the evidence of relict colonies it was suggested that the last ice-invasion in the eastern states was followed by a period of drier and possibly warmer climate. More recently the pollen studies of Sears have shown that the sage-brush deserts of Wyoming, during this dry period, actually extended eastward as far as Iowa.

Surely it will not be long before we know the past history and distribution of plant life in our own country as well as it is now known in Europe, and with that knowledge we can explain the present facts of plant distribution far more adequately than ever before.

It has already been stated that the environment exerts an effect on the individual structure of plants. While it is clearly in the field of ecology to investigate this influence, it probably also devolves on the ecologist to reverse the problem and to explain the environment from the evidence of the plants. That has been done in a most brilliant way during the past twenty years by Douglass and his assistants in the west. From a study of the annual rate of growth of trees, as expressed in their annual rings of wood, Douglass has been able to derive a very satisfactory picture of the climate in the west for the past thousand years, and a reasonable idea of it back to the beginning of the Christian era. Long periods of favorable climate alternate with long periods of deficient climate, and all of these must have been directly associated with the advance or the retreat of species of animals and plants, as well as with significant events in the history of the Indians.

The impressive work of Fernald in Newfoundland and eastern Canada is another example of the use of phytogeographic evidence in other lines of science. Fernald's discovery of numerous isolated colonies of far-western species in many localities from Lake Superior to the Atlantic suggests to the ecologist a uniform preglacial flora extending across the continent in these latitudes, followed by an interglacial or early post-glacial differentiation. It also indicates to the geologist that the great ice-sheet of Wisconsin age was not continuous, covering our northeast with an ice-blanket a mile thick, but

that the ice flowed as rivers around our mountains and higher hills, leaving uncovered these scattered areas upon which a preglacial flora existed, and where preglacial species persist even to the present day.

Our quarter-century has also seen the rise and fall of another hypothesis of great interest, not entirely unconnected with the problems of plant geography. That is the Age and Area theory of Willis, which held, in general, that the older the species, the greater is its geographical range. If true, the theory gave us an immediate and direct means for determining which are the old or parent species and which are the young species, derived from the old ones by recent evolution. It is obvious that such knowledge would be of the greatest value to taxonomists. While every one was willing to admit the theoretical truth of such a statement, there seemed to be so many other factors which might accelerate or retard migration from the center of origin, and so many vicissitudes which might actually cause the retreat of a species and the contraction of its range, that the specific applicability of the Age and Area theory to any small group of plants might be seriously questioned.

Still another theory of compelling interest has been published during our quarter-century which is of immediate interest in plant geography. This is the Wegener theory of continental drift. Geologically, it holds that the present continents were formerly all adjacent and that they have gradually drifted apart into their present position. Certainly the configuration of the continents shows how they may once have fitted together. If the continents have so drifted apart, and if the separation began after angiospermous plants came into existence, the theory would go far toward explaining many of the similarities and differences between the continental floras. It would easily account for some resemblances between the floras of tropical South America and western Africa, or between those of southern South America and New Zealand. Unfortunately, the theory requires a shifting of the location of the poles in a way which does considerable violence to botanical and geological facts, and as a result the theory of continental drift has gained few adherents among botanists.

In conclusion, let us attempt to summarize the problems of ecology as they exist today. The descriptive stage of the science, devoted primarily to amassing facts, has passed. The present task is the knowledge, the appreciation, and the logical explanation of all the phenomena of vegetation, including the grouping of plants into societies, the interactions of plants within these societies, and the distribution of species and of vegetation over the surface of the world. Much definite progress has been made; many unsolved questions are still under active study.

VIRUS DISEASES OF PLANTS: TWENTY-FIVE YEARS OF PROGRESS, 1910–1935

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Twenty-five years ago it was relatively easy for a student of plant pathology to learn what was then known concerning the virus diseases of plants. The literature was small and it reported few diseases. The agents causing these diseases had been shown to pass filters having pores so minute that they held back the smallest bacteria. Previous to this discovery, virus diseases were believed to be due to bacteria. Twenty-five years ago plant pathologists did not realize the great economic importance of virus diseases, and these diseases were somewhat neglected.

But virus diseases are no longer neglected, because plant growers all over the world have awakened to the fact that they cause serious losses. The change that has come about is reflected in a vast literature that has accumulated during the years under consideration. More than three thousand papers on virus diseases of plants have appeared during this period. This number does not include numerous short reports and casual references. A review of the literature reveals some interesting facts. About two thirds of the papers deal with the virus diseases of the following six plants: potato, sugar cane, tobacco, tomato, sugar beet, and cucumber. More than one third of the literature relates to the potato and sugar cane plants. Approximately one fourth of all the papers are on virus diseases of the potato. Why has so much work been done on the diseases of two plants? Both are extremely important as sources of food, but this alone can hardly account for the attention they have received. The answer is that the potato and sugar cane plants have probably suffered more seriously from these diseases than any other important crop plants. This is due partly to the fact that both plants are subject to a considerable number of serious virus diseases, and partly to the fact that both are propagated vegetatively.

Viruses are seldom transmitted through the true seeds of plants. Each new-born generation propagated from seeds is, as a rule, free of virus diseases, but vegetatively-propagated generations accumulate more and more of these diseases as the years go by. It is extremely difficult to find a single

potato plant in commercial fields that is free of the virus of latent mosaic, and many are infected by several different viruses. When a potato variety has accumulated so many different viruses that it can no longer survive commercially, it is said to have degenerated or run out. Plants such as these that have accumulated, or are in the process of accumulating, an assortment of viruses are not favorable material in which to study virus diseases. It is unfortunate that about one fourth of the work on virus diseases during the past twenty-five years should have been done on such an unfavorable plant as the potato. Hundreds of papers have been devoted to descriptions of virus diseases on different potato varieties growing under many different climatic conditions. The descriptions are frequently concerned with diseases caused by two or more different viruses, and too frequently this fact is not known or mentioned by the author. Better progress would have been made, undoubtedly, if potato viruses had been studied more and potato diseases less. Most, if not all, of these viruses affect a number of different species and can be studied separately in plants propagated from seeds.

However, considerable progress has been made in the control of potato and sugar cane virus diseases. Seed certification, roguing, tuber unit indexing, and the growing of isolated seed potato stud plots are some of the methods to which potato virus diseases have yielded. Somewhat similar methods for insuring clean seed have been adopted by sugar planters. Varieties of cane resistant to mosaic have been produced and are being grown in regions where this disease was formerly severe.

Ways have also been found of controlling, to a considerable extent, the virus diseases of tobacco, tomato, sugar beet, and cucumber. Much more care is taken now than formerly to avoid infecting tobacco plants when they are transplanted from the seed bed to the field. It was discovered that workmen, whose fingers become contaminated with the virus of tobacco mosaic from handling and using cigarettes and other forms of manufactured and raw tobacco, spread the disease when setting out young plants. Furnishing the workmen with sterilized tobacco has solved this problem. Certain virus diseases of the tomato are carried over winter on perennial weed hosts. Destruction of such weeds has reduced the incidence of disease in this crop. The curly top of sugar beets has, over a long period of years, caused heavy losses to beet growers and has proved difficult to control. The insect that spreads it is numerous and can live on a large number of different species of plants. However, varieties of sugar beets have been produced in recent years that resist this disease. It is believed that cucumber mosaic may eventually yield to a similar method of control, and that in due time the virus diseases attacking each of the six crops that, in the past, have suffered most will be

satisfactorily checked. Blight-resistant varieties of spinach have replaced the susceptible varieties formerly grown. Aster plants are protected from the insect that spreads the yellows disease by growing them in cloth-covered enclosures. Spread of the false blossom disease of cranberries is checked by spraying bogs with a contact insecticide which kills the vector. It has been found possible to cure young peach trees of the peach yellows disease by heat treatment. Still other methods have been devised for controlling the virus diseases of other plants, but time will not allow mention of these, for I wish to speak briefly of progress in other directions.

Students of virus diseases would like to know the nature of the filterable agents that so profoundly affect the health of plants. Are they minute organisms of some kind that will not grow and multiply in the absence of living host cells, or are they autocatalysts that possess a peculiar disease-producing potency? Twenty-five years of work have not brought answers to these questions. However, many interesting things have been learned regarding the behavior of viruses. It would be presumptuous to even attempt to list the important discoveries that belong in the field and to the period under consideration. A brief account will be given of some of the findings that seem to be important.

Cell inclusions associated with the tobacco mosaic disease were observed and described by Iwanowski many years ago, but the work was not confirmed until about fifteen years ago. It has recently been shown that characteristic inclusion bodies are associated with many, but not all, plant virus diseases. The bodies are small, plastic, vacuolate, amoeboid structures imbedded in the cytoplasm of affected cells. They show the staining reactions of protoplasm, and are usually closely associated with the plant cell nucleus. They occur in cells in the chlorotic tissues of mottled leaves. Although the significance of the bodies is not yet known, they are the most interesting structures that cytological studies of plant virus diseases have brought to light. They may represent a stage in the development of an etiological agent.

It is always important to know how a virus disease spreads, for the means of spread determines the season of spread, the rate of spread, and the range of spread. During the past twenty-five years the specific insect vectors of a score of important virus diseases have been discovered. To describe the interesting relationships that have been found to exist between these insects and the viruses they transmit would make a long story, but a few must be mentioned. Viruses causing eight different plant diseases have been shown to require an incubation period in the insects that transmit them. The virus of aster yellows furnishes a good example of this relationship. The leafhopper that spreads yellows to asters and many other plants is quite unable to trans-

mit virus immediately after first feeding on a diseased plant. A minimum period of ten days must elapse between the time when this insect first feeds on a diseased plant and the time when it is first capable of transmitting virus to healthy plants. Whether or not the infectious agent multiplies in the insect during the incubation period is not known. Another characteristic of specific insect vectors is that they retain the viruses they transmit over long periods of time. If a newly-hatched aster leafhopper is allowed to feed on a yellowed aster plant for a few hours, it may retain the virus as long as it lives, which is on an average about sixty days. During this period the insect passes through the five stages of development known as instars, becomes mature, and reaches old age. The virus has no detectable effect on the insect, and nothing is known regarding its location in the body of the insect. Storey was able to transmit the virus of streak of corn from leafhopper to leafhopper by means of needle punctures, and found that virus appears in the blood of infected insects. Viruses are not transmitted from adult insects to their offspring through eggs. Newly-hatched insects are virus-free. Only one exception is known. Virus of the dwarf disease of rice is transmitted to baby leafhoppers through eggs laid by infected females.

Another outstanding discovery of the period under consideration is that viruses generally produce primary lesions in plants. Since these agents are known only through their effects on plants, concentration of virus in different samples can be measured only through studies on infection. These studies are facilitated by the use of plants in which conspicuous primary lesions are produced. The use of primary lesions in infection studies has greatly promoted quantitative work on several different plant viruses.

Another interesting development has come about through the discovery of the existence of virus strains. It is now known that a considerable number of closely related strains of several different viruses exist in nature. Each causes symptoms that are somewhat different from all other strains in the group to which it belongs. The virus of tobacco mosaic may be cited as an example. Numerous strains of this virus occur in nature, and it has recently been shown that by appropriate methods other strains may be isolated from plants infected by the ordinary type of tobacco mosaic virus. The strains seem to arise through a process comparable to mutation.

It has been found that plants infected by certain virus diseases acquire immunity. If, for example, a plant of *Nicotiana sylvestris* be infected by a mild strain of tobacco mosaic, it becomes immune to severe strains of this disease. Healthy young plants that become infected with a certain strain of tobacco mosaic virus designated as 111D invariably die. If they become infected by a mild strain of tobacco mosaic before inoculation with the lethal

strain, they become immune to the latter. When it is realized that there are strains of tobacco mosaic so mild that they cause very little injury, the possibilities in this method of protecting plants become evident. The immune reaction is also valuable for the detection of relationships between different viruses. One further bit of work that must be mentioned is that which has shown that certain viruses, or substances closely associated with these viruses, are antigenic, and that serological reactions may be used in the identification and classification of viruses.

These are some of the steps in the progress that has been made in studies on virus diseases during the years since 1910.

TWENTY-FIVE YEARS OF SYSTEMATIC BOTANY, 1910–1935

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Systematic botany is the oldest branch of botanical science if we omit the applied phases such as agriculture and medicine, both of which long antedate any organized botanical science as such and date from the prehistoric period of the human race. Until well toward the middle of the past century plant science was practically limited to systematic botany; the numerous specialized phases such as physiology, pathology, histology, bacteriology, morphology, genetics, cytology, ecology, and forestry had not been developed or were of the most nebulous character. The development of these numerous specialized phases of botany, particularly the so-called laboratory sciences in modern times, has challenged the position of systematic botany, and has profoundly altered our outlook on the whole field of plant science. Yet in any comprehensive consideration of the wider field, taxonomy inevitably plays an indispensable part. It must be continued and strengthened because research in all other fields of practical, theoretical, and applied botany, no matter what their scope or character, cannot be disassociated from the names of the organisms with which the laboratory and field worker deals. To this degree those botanists working in other fields are dependent on the systematist whether they realize it or not. It may be conceded that the thing and its name are distinct but in discussion it is obviously impossible to disassociate the two.

It has been fashionable in some quarters in modern times to decry both the importance and the value of systematic botany. Because of its vitality, its human interest, its practical bearing on other phases of plant science, and on our every day life, one suspects that some of its critics have lacked the breadth of view of leaders in science, and have been misguided in criticising that which they did not fully understand.

It is suspected that the numerous changes in plant names, characteristic of the closing decade of the last century and the first two of the present one, and the long continued and sometimes acrimonious discussions of nomenclature characteristic of the same period, have in themselves tended to discredit taxonomy. These changes and these discussions, however, were only episodes in the modern development of this branch of plant science, indicating the

need of a critical examination of the basis on which taxonomy rests, and the necessity of certain changes if reasonable uniformity was to be established and maintained, and continued progress made.

What was the status of systematic botany twenty-five years ago? What are some of the outstanding accomplishments within that period of time? What are some of the fundamental problems that now confront taxonomists? What contributions have other branches of plant science made to taxonomy, and how are taxonomists applying these newer discoveries? Naturally not all of these, and other questions, can be answered in detail.

Twenty-five years ago the position and objectives of systematic botany were not fundamentally different from what they are to-day. Its numerous devotees in all countries were and are concerned with the proper identification of current collections; with the description of the numerous new forms constantly being collected in the lesser known parts of the world; with the adjustment of synonymy in their attempts to determine the proper application of the myriads of published binomials; with the preparation of monographic treatises covering major and minor groups; and with the preparation of descriptive floras covering large and small areas.

Objectives in monographic treatises include the preparation of critical descriptions of all known forms in the group under consideration; the accounting for all published binomials appertaining to the group; the delimitation of genera and subgenera, and of species, subspecies, varieties and forms; the determination of the known geographic range of each recognized unit; the association of all recognized units, large and small, in phylogenetic sequence showing the interrelationship of recognized units; and the preparation of keys to the recognized genera and species:—in fine, the compilation of all data bearing upon the subject under consideration and their presentation in orderly form. The ideal would be the preparation of a world flora in the form of monographic treatises, but the field is so vast, the available collections so extensive, the published data so scattered, the new forms constantly being found in all parts of the world so numerous that it not infrequently happens that a monographic treatise of outstanding excellence is obsolete even a few years after publication. The number of competent, well trained and experienced taxonomists so located in reference to available herbarium and library resources that they are in a position to accomplish productive work are relatively so few that progress is regrettably slow.

Early in the preceding century, when it became evident that it was manifestly beyond the power of any one man to handle the world flora in the sense that Linnaeus and his successors attempted in the various editions of the "Species Plantarum," various attempts were made to solve the problem by

monographic treatments. These were limited by the material that was available to their authors, when the various groups were studied. Some families were so treated in individual works. The two outstanding series of monographs in the nineteenth century were De Candolle's "Prodromus" and "Monographie Phanerogamarum," continued by three generations of the De Candolle family with the cooperation of numerous specialists from 1824 to 1896.

With the beginning of the present century Engler's project "Das Pflanzenreich" was launched, and from 1900 to 1909, there appeared in this series of monographic treatises detailed considerations of 46 families or parts of families, and within the past twenty-five years, from 1910 to date, 54 additional parts have appeared. This has been almost wholly the work of German taxonomists, contributions from other countries including one small family by an English botanist, two small families by an American, and a part of one medium sized family by a Belgian. Radlkofer's critical consideration of the Sapindaceae, published after his death at the advanced age of ninety-eight years, practically represents the life work of one man.

In the treatment of genera and species we have no modern counterpart of the monumental "Genera Plantarum" of Bentham and Hooker (1862–1883) where all groups of flowering plants, as to families and genera, were consistently treated by two individuals, actually for the most part the work of one. It was followed by the Engler and Prantl "Die natürlichen Pflanzenfamilien," a much more ambitious work, which covered all groups of plants, and appeared between the years 1887–1915. Being the work of very numerous specialists, it naturally lacks the uniformity of treatment of its great predecessor. Within the period with which we are now concerned the second edition of "Die natürlichen Pflanzenfamilien" is being issued, and between the years 1926 and 1935, 13 volumes have appeared. This is marked by a more uniform treatment and greater detail. Its completion will be a boon to systematic botany.

Following the publication of any authoritative treatment of families or genera, or an equally authoritative treatment of any single genus or family, or even an outstanding general or local flora, one notes a period of what may be called stagnation. Through the weight of authority the tendency is for a time to refer most current collections to genera and species described in such works. In monographic treatises those consulting them do not fully realize that the material available, let us say in 1900, in all the botanical institutions of the world, most inadequately represented the species of the world in that particular group. An excellent illustration of this point is supplied by Warburg's treatment of the Pandanaceae in 1900, wherein he recognized

3 genera and 190 species, with about 29 species so inadequately known that they could not be placed in relation to the recognized ones. Since 1900 about 370 new species have been described in this one relatively small family which is limited to the tropical regions of the Old World. This reflects very great field activity on the part of collectors. Within the present century they have secured nearly twice as many species as were obtained by their predecessors in the preceding two hundred years or more. How quicky a monographic treatment may be outdated is here beautifully illustrated; and yet, in 1900, Warburg's treatment was an excellent one for the described species actually represented in European herbaria at that time.

When Linnaeus issued the first edition of the "Species Plantarum" in 1753 he published 5,950 binomials; and ten years later he had increased this number to about 6,900. At the end of his publishing career but about 8,500 species had been named and characterized. This, then, was the approximate summary of all named and described species, under binomials, for the entire world in all groups of plants in 1780.

It is very doubtful if the average taxonomist, much less the average botanist, fully realizes the extent of the annual accretions of published binomials in modern times. Confining my statistics to the past twenty-five years, the life span of this institution, and again confining myself to two groups of plants only, the phanerogams and the ferns—and it must be remembered that activities in the lower groups such as algae, mosses, hepatics, lichens, and fungi have been relatively as great, perhaps greater than in the two groups I have selected—the following figures are significant.

New Binomials Published 1910–1935, Phanerogams and Ferns Only

New binomials published	Average per year	New species described	Average per year
162,500	6,500	118,700	4,750

The difference between 162,500 and 118,700, or 43,800, represents the approximate number of new combinations published by transfers of specific names from one genus to another, averaging 1,780 per year. In our times the annual accretions of new species described in all groups of plants, if we include the cellular cryptogams, equals or exceeds the total number of species known to Linnaeus, father of modern botany. About 162,000 new binomials published in the past twenty-five years for the ferns and flowering plants alone, contrasted to about 525,000 for the preceding one hundred and sixty years, indicates the tempo of modern publication in the realm of systematic

botany, the approximate total of published binomials to date, excluding the cellular cryptogams, being 687,000.

The figures are very significant. They indicate at once what a hopeless task it is for any one man to maintain even a good working knowledge of the enormous number of binomials and their accompanying descriptions, short and long, concise and diffuse, good, bad, and indifferent, that have been published since 1753, to say nothing of the many thousand new ones that are proposed annually.

The average systematic botanist has an intensive knowledge of only a few thousand species; some do not encompass more than a few hundred. It is exceptional for any one botanist to master the details of as many as 10,000 or 15,000 species, and very few individuals exceed these numbers. When it comes to a really critical knowledge of plants and their relationships it is doubtful if any but the individual with an extraordinary mind can claim that he really knows more than a few thousand species.

The average botanist has to depend on published floras. In this field, beside numerous local compilations, we may cite as coming within our period certain outstanding works, such as Hegi's "Illustrierte Flora von Mitteleuropa," 7 volumes (1906–1931); Komarov's "Flora U R S S" projected in 15 volumes of which 3 were issued in 1934; the continuation of the Dyer-Prain-Hill "Flora of Tropical Africa" bringing this major work measurably close to completion; Lecomte's "Flora générale de l'Indo-Chine" projected in 7 volumes and now three-fourths completed; Ridley's "Flora of the Malay Peninsula," 5 volumes (1922–25); and in our own country "The North American Flora" sponsored by The New York Botanical Garden, projected in 34 volumes of which 74 fascicles have been issued (1905–35); Rydberg's "Flora of the Rocky Mountains and Adjacent Plains" (1917), ed. 2 (1922), and "Flora of the Prairies and Plains of Central North America" (1932); Small's "Manual of the Southeastern Flora" (1933); Jepson's "Manual of the flowering plants of California" (1923–25); Abram's "Illustrated Flora of the Pacific States" projected in 3 volumes, volume 1 issued in 1923; and Marie-Victorin's "Flora Laurentienne" (1935). For the West Indies Britton & Millspaugh's "Bahama Flora" (1930) and Britton and Wilson's "Botany of Porto Rico and the Virgin Islands" (1923–30); and for Mexico Standley's "Trees and shrubs of Mexico" (1920–26). Time and space do not permit a further extension of this list, but it is noteworthy that for vast areas no comprehensive compilations are available, including much of Asia and Malaysia, Polynesia, and large parts of Africa, while for Australia, India, South Africa, Brazil, and Chili the floras published in the preceding century are all in need of modern revisions.

As an illustration of the bearing of active exploration on our knowledge of the flora of a region the Philippines may be cited. Here in 1900 in all groups less than 2,500 species were known, yet today approximately 14,000 species have been described, though not, unfortunately, thoroughly digested. With New Guinea the increase in our knowledge of the species has been even more remarkable, for many thousands of new ones have been described from that great island within the present century, an island less known botanically in 1900 than was the Philippine group.

The changing of generic names, sometimes unfortunately unavoidable, involves the publication of numerous new binomials. In some cases it becomes necessary to propose a new generic name for a large group, or to adopt some previously published one for the reason that the currently used one is invalid. In other cases generic concepts change and large collective genera such as *Panicum, Andropogon,* and *Quercus* are subdivided. Thus in *Quercus* in 1916, Koidzumi reinstated *Synaedrys* Lindley (1836) for a group of species largely developed in Asia, publishing 148 new binomials. Three years later Rehder adopted the earlier name *Lithocarpus* Blume (1825) for the same group and published 75 new binomials. In certain genera it becomes the fashion from time to time to segregate microspecies, as in the cases of *Hieracium, Rubus, Rosa,* and *Taraxacum* in Europe, and *Crataegus, Panicum* and *Iris* in the United States. In certain very large genera such as *Dryopteris, Selaginella, Polypodium, Eugenia, Ficus, Rhododendron, Primula* and *Panicum* continued field work constantly brings to light numerous undescribed species, or at least what active taxonomists take to be undescribed species, and the naming of these adds its quota to our constantly increasing list of binomials. Thus in *Rhododendron* alone within the present century in excess of 500 new species have been described from China alone. The nonspecialist who confidently proposes and describes new species in such complex genera as *Dryopteris* and *Selaginella* has no complaint to make when an individual really conversant with the group relegates his brain-children to synonymy; and this is the ultimate fate of most such ill-advised "new species."

An unfailing source of new binomials is the often ill-advised reduction of small genera to a single large collective genus and the equally ill-advised segregation of numerous small weak genera from a single large one. As an extreme illustration of the accretions to our already over-long list of new binomials, due to the reductions of currently recognized genera, we may cite the work of Krause on the Cruciferae and Umbelliferae of Europe.* In the

* Krause, E. H. L. in Sturm, J. Flora von Deutschland in Abbildungen nach der Natur, ed. 2, **6**: 1902. **12**: 1904.

first family he proposed the new generic name *Crucifera,* to include all genera of the family. He proposed 166 new binomials, and reduced to *Crucifera* all the northern European species in the following 56 genera: *Aethionema, Alyssum, Arabis, Aubretia, Barbarea, Berteroa, Biscutella, Boreava, Brassica, Bunias, Camelina, Capsella, Cardamine, Cardaria, Cheiranthus, Cochlearia, Conringia, Coronopus, Crambe, Dentaria, Diplotaxis, Draba, Erophila, Eruca, Erucaria, Erysimum, Euclidium, Hesperis, Hirshfieldia, Hornungia, Hutchinsia, Iberis, Ionopsidium, Isatis, Kernera, Konigia, Laelia, Lepidium, Lunaria, Malcomia, Myagrum, Nasturtium, Neslia, Petrocallis, Psilonema, Raphanus, Rapistrum, Roripa, Senebiera, Sinapis, Sisymbrium, Subularia, Syrenia, Teesdalea, Thlaspi,* and *Turritis.*

For the Umbelliferae Krause accepted the Linnaean generic name *Selenium,* and under it published 86 new binomials, reducing all of the northern European species in the following 39 currently accepted genera: *Aegopodium, Aethusa, Ammi, Anethum, Angelica, Apium, Athamanta, Berula, Bunium, Bupleurum, Carum, Chaerophyllum, Cicuta, Cnidium, Conium, Coriandrum, Cuminum, Daucus, Echinophora, Gaya, Heracleum, Pastinaca, Phellandrium, Pimpinella, Pleurospermum, Scandix, Sesli, Silaus, Sison, Sium, Smyrnium, Tordylum* and *Trinia.* In these two cases the genus was interpreted to be co-extensive with the two large families of plants, the Cruciferae and the Umbelliferae!

Opposed to this wholesale reduction of genera witness the work of Van Tieghem as contrasted to that of Bentham in the Loranthaceae. The latter in 1880 recognized 13 genera and the former in 1896 segregated 133 genera, most of them proposed as new and with few to many binomials in each. N. E. Brown segregated numerous new genera from *Mesembryanthemum.* Britton and Rose proposed many narrow segregates of genera in the *Cactaceae* and the *Caesalpinoideae.* Rydberg, Small, and others have made numerous generic segregates on very minor characters in various families. The aggregate number of changes in binomials proposed by both those who maintain narrow generic and specific segregates and those who incline to the treatment of very broad collective units is very great, and neither group wins many disciples. All systematists unhesitatingly agree that Krause's position was illogical in the extreme. A large majority of these would denounce the narrow generic segregates of the other individuals as equally illogical, adding to the confusion, and serving no good end.

As to the public, two groups are involved, the large non-botanical group, uninformed on plant names and relationships, and yet a public that must use plant names; and a small assemblage of professional, semi-professional, and amateur botanists. The first group is apt to be dazzled by the productive

output of an individual but has no criteria on which to base a judgment. Those in the last group for the most part bitterly resent illogical and ill-conceived changes in nomenclature that are forced upon them. After all the taxonomist who follows the dictates of good judgement; who adopts in his segregation of genera and species a reasonable attitude, being misled neither by the extreme " splitter " or the equally extreme " lumper "; who carefully weighs the evidence for and against segregation and combination; and who avoids the error of proposing and maintaining units, as genera, species, varieties or forms, that cannot by any criteria be differentiated by constant and tangible characters, is the individual who in the long run commands the respect of his botanical colleagues. The extremist is countenanced merely as an unavoidable irritant, whose opinions are not respected, and who is usually classed as Rafinesquian in commemoration of that brilliant but erratic American botanist, C. S. Rafinesque, of the first half of the preceding century.

De Candolle * in his consideration of enigmatic genera and species, in discussing the poor work of certain early botanists, notably Vellozo, Loureiro, and Blanco, remarks: " Il est à regretter que ces révérends ecclésiastiques, et même le Père Plumier, leur prédécesseur, ne se soient pas contentés d'écrire des homélies. Bonnes on les aurait lues, mauvaises on les aurait mises en côté; tandis qu'en histoire naturelle l'existence de certains noms et de certaines planches rend nécessaire de consulter indéfiniment les plus mauvais ouvrages."

There is no method of eliminating from consideration works of the type De Candolle so justly criticises. A genus or a species proposed with a formal description must be accounted for, no matter how inadequate, inaccurate, or misleading such a description may be. In modern times there are numerous cases of individuals who have published just as bad or even worse botanical papers than the pioneers that De Candolle condemns, and some even in the present century, such as Gandoger and Léveillé. The latter between 1894 and 1918 proposed and very inadequately described between 3,000 and 4,000 new species of plants, chiefly from China, in a series of usually short and widely scattered papers, involving perhaps 150 titles. A well known species of *Symplocos* originally described in 1784, he redescribed as three new species in *Crataegus, Prunus* and *Cotoneaster;* other species of *Symplocos,* all well known, he redescribed as new in *Litsea, Maesa,* and *Eurya.* A well known species of *Iodes* was redescribed as four new species in *Vitis, Sabia,* and *Hernandia.* Several old and well known species of *Ilex* were redescribed as new species in *Celastrus, Callicarpa, Embelia, Macsa, Myrsine,* and *Diospyros.* Other well known species of *Celastrus* were redescribed as new in *Saurauia, Embelia, Erythrospermum* and *Berberis.* A well known *Gardneria*

* La Phytographie 141. 1880.

was redescribed as four new species in *Sabia, Paederia, Marlea,* and *Rhamnus.* In the Verbenaceae * he ascribed to that family and described as new in various genera representatives of *Ilex, Dichroa, Colquhounia, Tacca, Viburnum, Meliosma, Hydrangea, and Buddleja,* representatives of seven families all unallied to the Verbenaceae. Yet these are only a very few of the gross and inexcusable errors made by this erratic botanist. Rehder's † critical paper based on an actual examination of Léveillé's types of woody plants indicate the magnitude of his errors. It is exceedingly doubtful if ten per cent of the several thousand new species Léveillé proposed will actually prove to be valid ones, for it is only by accident that any of them were actually " new " at the time he proposed them. Probably very few, perhaps none, of his numerous new species could definitely be placed from his inadequate descriptions alone. Yet under our present rules all of these numerous redescribed " species " must be critically considered by whoever happens to revise the groups in which they were too often erroneously placed, and they can definitely be placed only by a critical examination of his actual types. If botanists in other fields than taxonomy become exasperated with the taxonomists as a group for their nomenclatural and systematic vagaries and shortcomings, the taxonomists have equal justification in being exasperated at the erratic work of some of their own colleagues.

Past, and for that matter, much of the present-day work in systematic botany was and is based on various more or less standard concepts of comparative morphology. Within the present century numerous contributions have been made by various botanists, some of them taxonomists, some specialists in other fields, to the problems of systematic botany.

Thus, in field studies the intensive work of Wherry in the correlation of morphological characters of plants with a definite type of environment, usually the soil, is a typical and important contribution to systematic botany. Fernald's critical field studies of relic species in relation to glaciated areas in North America have been outstanding, contributing definitely to systematic botany on the one hand and on the other radically modifying some rather generally accepted geological ideas in regard to the extent and continuity of the great ice sheets in times immediately preceding the present. Allan's field work in New Zealand and Wiegand's in the eastern United States on the occurrence of hybrids in nature has contributed materially to the elucidation of certain puzzling problems in reference to the limits of some species. An-

* Merrill, E. D. Sinensia Spec. Bull. 9. 1930.

† Rehder, A. Notes on the ligneous plants described by H. Léveillé from eastern Asia. Journ. Arnold Arb. **10**: 108–132, 184–196. 1929; **12**: 275–381. 1931; **13**: 299–332. 1932; **14**: 223–252. 1933; **15**: 91–117, 269–326. 1934; **16**: 311–340. 1935.

other phase of field work that deserves mention is the dawning realization of the fact that an intensive exploration of classical regions, that is those areas from which the types of the early described species actually came, yields unexpectedly important data tending to the better elucidation of what was actually intended by certain short, generalized, early descriptions. Such work not infrequently shows that current interpretations of certain more or less classical species may be erroneous in the extreme.

In the application of genetics and cytology to systematic botany we have the contributions of individuals such as Babcock, Anderson, Keck, and others. Cytological analyses of species-hybrids, of suspected hybrids, and of what on morphological grounds were considered to be true species, contribute materially to our knowledge of species limits in various groups of plants, and explain much that was obscure when judged on strictly morphological grounds. Contributions from this field indicate the necessity or desirability of reducing certain formerly recognized species, and in other cases, the equal necessity or desirability of segregating two or more species from what was formerly considered to be a single one.

In still other fields, such as the work of Record in wood anatomy, that of Wodehouse on the structure and classification of pollen grains, the transplant work of the late H. M. Hall, and possibly even the serum-diagnosis work of Mez contribute to the solution of the problems of the systematic botanist.

All of these methods, and others, while yielding valuable results, in themselves for the most part require so much time, that none of them can possibly replace the usual morphological criteria used in the differentiation and characterization of species. Most frequently they merely serve to confirm the prevailing opinion among taxonomists as to the limits of this or that species as originally constituted on morphological characters. It is indeed striking how often intensive laboratory and field work, perhaps originally undertaken with the motive of disproving this or that tenet set up by the taxonomists, tends to confirm the correctness of the concept of what we may call the traditional species.

What is a species? All we can say is that it is a subjective concept rather than an objective reality. There is the well known dictum that species as such do not exist in nature. All so-called species vary much or little, and no two specimens of any accepted species are exactly alike in all respects. Variation is the rule, not the exception. Some modernists claim that the word species should be abandoned as being out-dated, and advocate such terms as phenotype or morph as a substsitute, words which implicate nothing more than visible differences between organisms; but phenotypes and morphs would need have names, even as do species. Until some outstanding investigator

can propose a better alternative scheme, superior in both practice and theory to our present species-concept, we will have to bear with our present terminology, in spite of its faults. After all some system is better than chaos, and if some believe systematic botany is chaotic, this must be largely because they are unfamiliar with the really, on the whole, orderly arrangement of the plant kingdom in major and minor groups, orders, families, genera, and species, even though these units, as to their limits, be largely concepts of the human mind.

Nomenclature cannot be dissociated from taxonomy. No matter what the field of research of the individual may be, he must of necessity consider the names of plants. For various reasons the same genus and the same species has frequently been described under different names, until synonomy has become a vast and exceedingly complex subject. Botany not being an exact science there has and doubtless always will be differences of opinion even among specialists as to family, genus, and species limits. At times, and with certain botanists always, there is the tendency to extensive segregation of both genera and species, and conversely the trend on the part of others to combine weak and not sharply defined genera and species in more or less collective groups. The pendulum swings back and forth over a period of years; it is the old play of radicalism versus conservatism. It is one man's opinion and judgment against another's involving personal elements not subject to any legislation.

In a very recent and extensive treatment of all the known grasses of the United States * it is noted that for certain species numerous synonyms are given. Thus *Triodia flava* (L.) Smyth has 38 synonyms, *Sphenopholis obtusata* (Michx.) Scribn. 33, *Bouteloua simplex* Lag. 28, and *B. curtipendula* (Michx.) Torr. 24. These are indigenous species that a hundred years ago or so had only one published name. More widely distributed ones such as *Setaria geniculata* (Lam.) Beauv. (73 synonyms), *Koeleria cristata* (Linn.) Pers. (41 synonyms), and *Echinochloa crusgalli* (Linn.) Beauv. (including 3 varieties, 46 synonyms), are even more impressive, but if all of the European and Asiatic synonyms of these widely distributed grasses be added, the numbers would be very greatly increased. These data, and similar figures are to be found in other groups of plants, clearly indicate the complexity of the problem, and the imperative need of fairly definite rules in selecting accepted names.

Beginning in the last decade of the preceding century radical changes were made in the names of plants, strict priority in the date of publication being the basis of most of these changes. Thus in Otto Kuntze's "Revisio Gene-

* Hitchcock, A. S. Manual of the grasses of the United States. U. S. Dept. Agr. Miscel. Publ. **200**: 1–1039. *f. 1–1696.* 1935.

rum Plantarum" (1891–1898) more than 25,000 new binomials were published. These numerous proposed changes were not acceptable to two groups of botanists, the conservative element that naturally reacted against any changes in currently accepted names, and that group that could not accept the beginning date of publication proposed by Kuntze. Soon we had three fairly well established schools: first the ultra-conservative group, that wished to maintain the nomenclature established by current usage, retaining the names and their application as established by usage in the nineteenth century; second a conservative group that would by legislation reject certain generic names; and third the radical group that argued on the basis of strict priority in publication as exemplified by the so-called American Code, and some of the supporters of the last group even out-Kuntzed Kuntze, in seeking beginning dates for generic names in the classical literature of the Greeks and the Romans. The arguments pro and con among the supporters of the various codes largely antedate the period with which we are dealing, covering the last decade of the preceding century and the first decade of the present one. Gradually sentiment more or less crystallized in favor of the International Code, many of its supporters coming to realize that certain provisions of the American Code were superior to and in advance of those of the International one. The modifications of the International Code adopted at the International Botanical Congress at Cambridge in 1930, whereby certain principles of the American Code were accepted, brought the two measurably close except in the one point of conserved generic names, and has won the adherence of the vast majority of taxonomists to the International Code in general. Except in the cases of a very few individual botanists, the so-called American Code has become merely a historical episode in our attempts to stabilize nomenclature. Under any code, where the rules are consistently applied, changes are inevitable, but we now seem to be approaching a period of stability in the application of binomials after a half century of discussion, flux, and change.

In the popular mind a botanist is an individual who knows and can name plants. A hundred years ago this was a true definition. It no longer applies because of the great specialization that has been developed within the broad field of plant science in the past seventy-five years. It would be the height of folly to insist that all botanists should master the field of systematic botany. This is neither necessary nor desirable. Yet it can be maintained as a general truth that the individual investigator, no matter what his field, who has a reasonable knowledge of the names and relationships of the organisms with which he deals, is a bette equipped individual for productive work within his own field, and that the teacher of botany who has the same knowledge is a better teacher. This is not always fully realized even by many of our most highly trained and effective men.

The tremendous developments of the past hundred and fifty years in our knowledge of the world's vegetation, the wealth of reference material available in the public and private herbaria in leading countries, the vast and complicated literature of world botany, all testify to the inexhaustible vitality of this, the oldest branch of botanical science. Thus in the field of systematic botany covering the higher groups of plants, from 1910 to 1935, as noted above, nearly 120,000 new species of plants have been described, averaging at least 4,800 per year.

Is it any wonder then, that as various special fields of investigation have been developed outside of taxonomy, within this field we have the same marked tendency to specialization? Thus we have individuals limiting their studies to the floras of limited areas and limited groups, and not infrequently, we find an individual making his life work the mastery of one single family, or even a part of a family, or one natural group as represented in some particular part of the world.

The practical importance of taxonomy is very great and from its very nature will continue to be so. It is one phase of botany that covers the entire field of plant science and impinges on all of the other biological sciences, and on the everyday life of all advanced peoples. In agronomy, in forestry, in pharmacology, in horticulture, in the practical phases of conservation, in commerce, in government, in many of the most ordinary walks of life we are constantly faced with the necessity of determining the name and relationships of this or that plant species. On the accuracy of the identification much may depend. We must therefore have available in our public and private institutions, botanical gardens, arboreta, museums, colleges and universities, a corps of trained and experienced taxonomists, competent to meet that constantly increasing need for making accurate identifications of plants.

In the field of pure science, much depends on taxonomy. While it is true that in the practical needs of our modern life the demands for the accurate identifications of plants are largely in relation to those species of economic or potential economic importance, the criterion of relative economic importance has no place in the mind of the experienced taxonomist. Much of the best work is done in groups of little or no practical value, but in these groups there is always the contribution to pure science, and in no matter what the group, there is always the chance that developments on other fields may show that a group of plants that was considered to have no practical bearing on the affairs of everyday life may be found to be of very great importance. And thus the taxonomist works in his chosen field, in the classification of the algae, fungi, mosses, hepaticae, pteridophytes and the great group of flowering plants primarily without thought of the practical bearing of his investigations, but

with the objective of bringing order out of chaos; to determine the limits of families, genera, species and varieties; to determine in the complex field of synonymy the valid and acceptable names for the myriads of species with which he is concerned; and to arrange his findings in orderly sequence, so that they will be available to contemporary and future scientists. He, like investigators in other fields, is interested in his particular branch of botany from the standpoint of science. If his investigations bear on the more practical problems of our daily life well and good. He cannot, and should not be expected to be wholly utilitarian, but should be encouraged and supported in his efforts to contribute to the sum of human knowledge, for after all knowledge is power and the taxonomist has his legitimate place in the scheme of things as they are.

TWENTY-FIVE YEARS OF FORESTRY, 1910–1935

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A quarter of a century ago a broad conception of the need and usefulness of forests was well intrenched in the public mind as part of a program of conservation of our natural resources. A national forest policy had become a reality under Theodore Roosevelt, its vigorous proponent from the time he became President in 1901. Progress had been swift during his presidency in creating national forests from the public domain under the forest reserve policy established by the Act of March 1891. He added more than 100 million acres to our National Forests between 1905 and 1909. The net area in that year stood at approximately 172 million acres. It can unreservedly be said that the policy of creating and managing national forests was firmly established by 1910.

Beginning in 1905 the Forest Service of the Department of Agriculture was chiefly engaged in placing these vast areas under management. Few people realize that for more than twenty-five years we have had a most notable example of wise land use in this great area carved out of the public domain, managed with the idea of fullest use of this natural resource including timber, water, forage, recreational enjoyment and other resources made available not only to nearby communities but to the nation as a whole.

Up to 1910 no other president had so effectively made the public conscious of the country's natural resources and their importance. The National Conservation Commission appointed by Theodore Roosevelt in 1907 presented the first comprehensive inventory of resources such as timber, coal and other minerals, soil and water. The thought uppermost in mind then was whether the supply would last a rapidly growing nation. Conservative use was the dominating note. The annual drain on our forests was disclosed and also the gap that existed between production of the forests and consumption of wood products—the latter being much greater than the total growth per year. Means of eliminating or reducing losses and waste were emphasized.

The President placed the facts collected by the Conservation Commission before the conference of State Governors which he called in 1908. Some states had already made considerable progress in formulating a forest policy and putting it into effect. Others were being roused to action.

At the time of the founding of the Brooklyn Botanic Garden, whose twenty-fifth anniversary we celebrate today, forestry had already made considerable progress and had just passed its first great peak. Notwithstanding the advance of federal forestry and the good progress made in certain states, much was wanting in its application. Important as these gains had been, the ensuing twenty-five years reveal a series of steps in advance that culminated in a second great peak of interest in forestry but from a different standpoint respecting the usefulness of forests.

At the beginning of the period there was a firm determination to advance the practice of forestry with nearly equal emphasis on federal, state and private activity. In reviewing the twenty-five years it is especially interesting to see the progressive ways in which this goal of accomplishment was sought.

Between 1905 and 1910 the Forest Service offered its services to the states in formulating forest policy and made studies of forest conditions upon application for this assistance. Recommendations of the Forest Service usually covered the following:

> "The appointment of a state forester or a forestry bureau to supervise the forest work of the state and to cooperate with private owners in assisting them to manage their forest lands properly; the enactment of laws for the protection of forest lands from fire by establishing fire warden systems, placing reasonable restrictions upon the use of fire, and providing suitable penalties for their infraction; the adjustment of taxes on forest lands so as to encourage the private owner to cut his timber conservatively and retain the land for future production; and the purchase or retention by the state of timbered or cut-over lands suitable for permanent state forests."

Valuable as this assistance was, it was purely advisory and development of state forestry depended on progressive leadership within the states concerned.

An effective means of stimulating state action became possible through a new policy established by the Weeks Law of 1911. Under this law $200,000 was appropriated by the Federal Government for cooperation with the states in protecting the forested watersheds of navigable streams from fire, a national menace.

This cooperation applied only to states that had provided for protection from forest fires and that had funds appropriated for that purpose; this in itself created a motive for state activity. It required an equal contribution of funds and carried with it, by agreement, federal inspection of the operation and efficiency of the cooperative system of protection. This was, I believe, the first federal law that ca .ied direct financial assistance to states on a 50-50 basis.

This measure confirmed and expanded by subsequent acts is outstanding

in the history of this past quarter century and has resulted in nation-wide protection of forests from fire. With advances in forest protection, it seemed as if the greatest obstacle to private forest practice had been removed.

Through this same law provision was also made to acquire national forests by purchase of lands on watersheds of navigable streams. The inauguration of this policy was of great significance since it made possible, through congressional appropriations, the purchase of large areas in the White Mountains, and in the Southern Appalachians for national forests.

The great bulk of national forests lay in the West comprising public lands wholly or partly bearing forests which had been set aside, as the law read, "To improve and protect the forest . . . for the purpose of maintaining favorable conditions of water flow and to furnish a continuous supply of timber for the use and necessities of citizens of the United States." This protective value was the chief argument in bringing about the enlarged policy of purchase and brought to the East benefits already recognized in the West.

From 1910 to 1920 national forests were increased by purchases in the East and decreased by land classification and boundary adjustments resulting in the elimination of several million acres from national forests in the West. That decade may well be described as one of consolidation of gains with progress in state activity and steady, continuous protection and technical management of national forests.

However, it became evident that forestry on public lands could not alone provide the benefits desired for the reason that approximately four-fifths of the forest area of the United States was in private hands. Depletion without adequate provision for re-growth still continued on private lands. The public rediscovered, so to speak, that private forestry practice was negligible as yet. Possibly the people were looking through the reverse end of the field glasses.

The Forest Service of the United States Department of Agriculture emphasized in 1920 the need to adopt a policy of enlarging the program of public acquisition of forests by the Federal Government, by the states, by lesser political divisions and of increasing the protection of forests from controllable losses such as fire and of perpetuating forest growth on all privately owned lands. Much was said and written. Conferences and committee reports abounded dealing with a situation that was viewed with alarm. It was not unlike a "revival" meeting in which the sins of depletion and devastation received terrific excoriation and the fires of a timber-famine-hell were made as vivid as the preacher's hell of old.

The public gained the impression that mandatory powers were to be invoked. Indeed there were bills before Congress calling for direct federal control of private forests and for indirect federal control of private forest

lands under the police power of the states; in the latter case the federal government was to function as a cooperating and standardizing agency. Neither of these measures passed and the result of the revival was to bring realization that a comprehensive national program was needed. Of equal significance was the official recognition of the idea that forest production is governed by economic laws and that any requirements of the private owner must be practicable from a business standpoint.

Investigations and economic studies made by the Forest Service resulted in a series of useful publications dealing with timber growing and logging practice in the various forest regions of the country. These emphasized the minimum requirements to keep the forest productive and the possibilities of more intensive forest practices. A senate committee investigated forest conditions and congressional attention was focused in 1923 on reforestation. Establishing forests on idle land by planting had been gathering momentum for more than a decade and at that time twelve states were maintaining nurseries and distributing trees for private reforestation.

Many states had also been giving woodland owners assistance in the practice of forestry. Since farm woodlots constituted about a third of the total forest area of the country, these seemed to offer a field for advancement of natural reforestation of privately owned forest land.

Here was the chance, it was thought, to step up the rate of progress in application of forestry. Small owners could do things that owners of large tracts with heavy investment might not economically be able to do. Agricultural extension work had done much for improvement of other crops and why not link the farm woodlot to the same service already developed? This was the next step.

The Clarke-McNary Law passed in 1924 authorized expenditures by the federal government in cooperating with the states in distribution of forest nursery stock for planting woodlots and shelterbelts, and in assisting farmers in managing their forest lands on a basis of continuous production.

This law also enlarged federal forest policy in advance of the provision of the Week's Law, its predecessor. The limitation of cooperative protection of forest lands to the watersheds of navigable streams was removed. This meant nation-wide action with the evident determination to reduce this obstacle to private forestry practice. It provided also for investigation of forest taxation which had been likewise regarded as an obstacle.

The year 1927 was one in which disastrous floods focused the public mind on the need to remedy the causes. Since the forest cover on principal watersheds constituted a factor of influence, this situation was influential in reinforcing the policy of federal acquisition of land. In 1928 legal provision was made for increased activity in this line.

Progress in forestry in the states during that decade was rapid, especially because of federal assistance already mentioned and the cumulative effect of continuous efforts and publicity year after year. Many states by that time had well organized state departments, had acquired state forests, increased efficiency of protection from fires, given aid through the extension service to private owners in woodlot management and in planting of forests.

A potent influence on progress in reforestation has been the abandonment of farm lands. It has been occurring for a very long time but most rapidly during the past twenty-five years. The causes are well known and need not be discussed. The process has been going on in all agricultural states to a greater or less extent and the aggregate acreage is enormous.

New York State took the lead in attacking this problem in connection with its enlarged forestry program. Through constitutional amendment, the so-called Hewitt Amendment which was passed following a report by a Commission on Reforestation, provision was made for acquiring by purchase and planting with forest trees a million acres of this land which had become unprofitable for agriculture. The plan provided for an annual program of planting over a period of fourteen years. From data furnished by the Conservation Department of the state, the 1934 record shows that 38 million trees in round numbers were planted on the reforestation areas alone.

Economic studies in various states have similarly pointed the way toward state planning with particular respect to determination of land classes and the fullest use of natural resources for the benefit and enjoyment of the people.

The next angle of approach to the solution of the problems of forestry on public and private lands, concurrent with reforestation activities, was a comprehensive program of research. It was an outgrowth of a demand for technical information on which to build sound timber-growing policies and practices.

Research in forestry was not new. The Forest Service had established its first experiment station near Flagstaff, Arizona in 1908 and a few similar establishments on national forests in the West at strategic points but on a rather meager basis of support. In 1915 it organized a separate research branch in the central office at Washington, thus emphasizing further the importance of investigative work and laying the foundation for the expansion that came with the passage of the McSweeney-McNary Law in 1928. This law provided for a long-time program of fundamental research by five government bureaus. To the Forest Service was assigned the Forest Experiment Stations, forest range research, and forest products. In passing, one may note that the Service had already done notable work in its Forest Products Laboratory at Madison, Wis.

Other government bureaus were to advance investigations of tree diseases and their control, forest insects and the means of the prevention and control of infestations, wild-life studies, and climatological investigations, particularly in relation to forest fire control. This may be considered the most significant and serious attempt yet undertaken to solve the problems of forest practice because it sought to get at the facts that underlie effective practices and replace methods of trial and error. Its comprehensive character and the scale on which it was undertaken are noteworthy. Ten Forest Service Experiment Stations, one in each forest region of the United States, have been in operation since this Act was passed and have justified this most important means of progress.

During the quarter century, research in forestry has not been confined to federal activity but has been in progress in educational institutions, state experiment stations and by private foundations. Schools of forestry have contributed in research and as well in demonstration of forest practices. Nearby examples in the East that are of great value are the Harvard Forest at Petersham, Mass., the Yale Forest at Keene, N. H., and the Pack Demonstration Forest at Warrensburg which is under the New York State College of Forestry at Syracuse University.

Contemporaneous with these developments has been the application of sustained yield management in national forests and to a lesser degree in state forests, the introduction of silvicultural practices in many farmers' woodlots and in a few notable instances forest management of private timber tracts looking toward continuous production.

The principle of sustained yield management in a given forest is to limit average annual cut to the continuous annual growth capacity. It has been frequently stated that the application of forest management with the objective of sustained production would solve America's forest problems. These considerations, broadly, are how can we meet continuously the Nation's needs for the products of the forest, keep up a steady flow of these from forest soils by repeated cropping under good silvicultural practices, and thereby make communities permanent and stabilize industries.

Economic investigations of land utilization have revealed the instability of ownership of much privately owned forest land. The forest industries during the period between the World War and the economic depression beginning in 1929 suffered from over-production. It was this troubled condition of the lumber industry that gave rise to the appointment of a Timber Conservation Board by President Hoover in 1930 to try to find a remedy. This Board brought together considerable material bearing on the situation.

A more exhaustive investigation was made by the Forest Service in 1932

in response to Senate Resolution 175 introduced by Senator Copeland of New York. The report recommends the assumption of full public responsibility for half of the commercial forest land, that is, half the timber growing task, five-sixths of the non-commercial forest land, three-fifths of the forest ranges, four-fifths of the area of major influence on watershed protection and eight-ninths of the areas which should be set aside for forest recreation. Public interest and public responsibility outweighed the considerations regarding private forest management, and the means of its profitable employment.

Space does not permit review of the exhaustive details of the report. It brings out the ultimate objective of obtaining "all the economic and social benefits which productive forest land and adequate timber and other products and services can bring." I quote this statement from a paper presented before the Society of American Foresters in order to give a background for the next great peak of interest and action in the progress of forestry. Stagnation of industry, unemployment and like evils need no comment to those who have had to face the conditions of the past five years. In 1932 forestry work became the means of using the unemployed both in federal and state work. Franklin D. Roosevelt in a letter to the publisher of the "West Coast Lumberman" in October 1932 elaborated his ideas concerning reforestation briefly discussed in his acceptance speech. In that letter he pointed out that "the care and enlargement of the forests of the Nation offer a promising and profitable field for the employment of idle men." He further said, "Apart from the present emergency I think we need a more definite and comprehensive national plan for protecting, conserving and enlarging our forest resources. This plan should have among its objectives more effective stabilization of the forest products industries."

Immediate action followed Franklin D. Roosevelt's inauguration in the establishment of the Civilian Conservation Corps that put 300,000 young men into the field of forestry as laborers. This was the second great peak in the history of the forestry movement. The effect in the progress of federal and state forestry can readily be appreciated. Out of a clear sky, so to speak, an immense labor force and an adequate equipment appeared to do the work of forest improvement.

As a social experiment this emergency conservation work has been a great success. It has helped the workers physically and mentally. It has changed the attitude from discouragement to confidence in life. The advent of this enormous labor battalion has put the forests and parks of the country years ahead in the program of efficient management and usefulness. Roads, trails, stand improvement, reforestation and the like have gone forward in great strides. Perhaps by far the greatest accomplishment has been the value this

work has had in giving the workers an appreciation of conservation and the public a better understanding of its significance. The social value of forests as a place for useful work has been given a new interpretation. It has become a known fact not a stated theory. In a recent report of the Forester of the U. S. Forest Service, he states that carefully considered plans indicate the need for at least 20 million man-days of work annually for years to come on the federally managed properties.

A second great feature of this emergency period has been the allocation of millions to increase the National Forest area. A news release from the Forest Service in March 1935 stated that 8½ million acres had been added to eastern forests. A recent bill in Congress for the federal government to aid the states in procurement of state forest areas seems to indicate a trend toward additional state ownership.

The lumber industry, like other industries, came under the National Recovery Act.* From the standpoint of forestry the most significant part was Article X, "The applicant industries undertake, in cooperation with public and other agencies, to carry out such practicable measures as may be necessary for the disclosed purposes of this code in respect to conservation and sustained production of forest resources."

Under this provision acceptable rules of forest practices were made for the various timber regions by the industry members. Considerable progress was made in putting these into effect notably in the Pacific Northwest and in the South. There is a lag at the present due to uncertainties until Congress, now in session, acts concerning the N. R. A. It is felt, however, that the essential values of Article X and the practice rules are likely to be continued. If this provision is continued it will constitute one of the great steps of advance in the management of private forest lands.

Emphasis should not be placed to so great a degree on federal forestry as to diminish either state or private activity. There must be a degree of independent state action and of private initiative in forestry.

The State of New York has shown a high degree of independence in its history that is worthy of note. Today is the Fiftieth Anniversary of the passage of the first comprehensive state forest administration law in America. It was on May 15, 1885, that the Governor of New York State signed a bill creating the Forest Commission. The State owned 715,267 acres of land in that year and has secured since that year by purchase and otherwise additional areas so that the total is 2,369,234 acres. In the same year, 1885, the State acquired the land adjoining Niagara Falls on the American side.

* Subsequent to the presentation of this paper the United States Supreme Court announced its decision on May 27, 1935 that this act was unconstitutional.

New York has never encouraged the acquirement of national forests within its boundary. It has conserved the wonderful forests of the Adirondacks and Catskills, protecting them from fire and trespass, arch enemies of former days. It has made them the paradise of those who love wild places. The state has developed within a quarter century a remarkable state park system to meet the rising tide of travellers to beauty spots for recreation.

Productive forestry has not been neglected. Protection of forests from fire has been extended where it was critically needed. Reforestation is reclothing abandoned farm lands. These things and many others mark the consistent, steady advance in meeting the State's forest and land problems.

In line with the national planning the most notable step in advance is the act making permanent a State Planning Board which will be a clearing house and a guide for well-ordered and wise progress in maintaining New York State's wealth of natural resources and their wise use for the maximum advantage of its citizens.

TWENTY-FIVE YEARS OF PLANT PHYSIOLOGY, 1910–1935

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Two persons have an element of danger attached to their utterances—the historian and the prophet. The historian may meet objection from those who weigh occurrences of the past in a different balance from that used by himself. The prophet is in an even more dangerous position, because the hold of the future on the past is none too stable a one, and the future sometimes breaks sharply with the past. However, while this applies to the world of politics, as we have seen, it would seem less likely to happen in the world of science. Still, it is possible even here, because one hardly knows what the development of the sister sciences may bring by way of new viewpoints and new methods.

In the hope of getting a starting point, I would like to review in an outline way the situation with Plant Physiology twenty-five years ago.

Twenty-five years ago, plant physiology was one of the younger children of the botanical family, and it existed rather independently of the older members—taxonomy and anatomy. These separate branches made relatively little use of each other, but during the past twenty-five years, while individual botanists have specialized and drifted apart until almost out of touch with each other at times, the subject of Botany as a whole has been slowly developing a unity through the recognition of mutually helpful relations.

By the methods of physiology a complete and coherent system of plant relationships has been built up by Metz and his fellow-workers at Königsberg. Taxonomy and physiology have thus come closer together, and since the results of taxonomy based on physiology agree closely with the scheme of relationships worked out on structural relations, these latter are seen also to be involved in the synthesis.

Formerly, the plant pathologist studied his disease-producing organisms quite apart from the reaction that the parasitized host might develop, and it was not until the chief aspects of the physiology of the parasite had become fairly well known that the host reaction—the physiology of the thing parasitized—has come to attract attention. The relation now between physiology and pathology is very close. The host reaction is being studied and predisposing causes are being sought in the environment through the physiologi-

cal conduct of the host under given circumstances. More and more, a physiological basis is recognized as necessary to a sound pathology.

Of course, I hardly need mention the fact that agriculture and all practical aspects of plant cultivation have long been known to reflect the great facts of physiology, and it was not by accident that physiology made its first great gains in institutions investigating the problems of agriculture.

When the Brooklyn Botanic Garden was established, plant physiology had already come out of the rather larval condition which characterized its earlier development in America. During the preceding twenty-five years—1885 to 1910—plant physiology was already receiving recognition in a number of the more prominent American universities. However, it differed from other phases of botany in America in that it had a rather more direct relation with Europe, particularly Germany, than other phases of the science had. A few Americans, studying with Sachs and Pfeffer, had brought to this country much of the German methods and some of the German viewpoints, and American physiology twenty-five years ago was continuing to build directly on the foundations laid in Europe.

Let me list some of the men and the problems in which conspicuous progress was being made in a period centering around 1910.

PHOTOSYNTHESIS

Perhaps one of the most important things was the work of Willstätter and his associates on chlorophyll. Chlorophyll had already been investigated from the standpoint of its general methods of functioning, but the chemical make-up of chlorophyll itself still remained uncertain. Willstätter, associated with Stoll and other of his contemporaries, put the chemical understanding of chlorophyll on a sound basis at this period. The knowledge of the action of chlorophyll was advanced by Lubimenko and Stahl, who studied it mainly from the ecological standpoint. Along with the clearing up of chlorophyll chemistry, conspicuous progress had already been made in the investigation of the physiological processes dependent on chlorophyll. Bäyer had advanced his formaldehyde-condensation theory of the origin of glucose in 1864. Brown and Morris in 1893 had claimed priority for cane sugar as the first carbohydrate; Dixon and Mason in 1916 were proposing an alternative. Some doubt still remained as to what the first carbohydrate found in plants might be.

Twenty-five years ago the presence of formaldehyde in the green parts of plants was receiving close attention from Schryver in America and from Curtius, Franzen and Grafe in Germany.

Other plant pigments were also receiving more thorough attention than before. Escher, working on carotin and lycopin, Hanson studying phycoerythrin, Molisch investigating purple bacteria, illustrated this greater interest in pigments.

CHEMOSYNTHESIS

Along with the work on chlorophyll and its significance for green plants, we may recall that chemosynthesis, developed in various of the minor organisms, was also receiving attention. The work of Molisch on sulphur and iron bacteria, the work of Lieske on iron bacteria, and Nikelewski's work on hydrogen oxidation, would illustrate this phase of plant physiology.

SOIL PHYSIOLOGY

Twenty-five years ago, the soil was being investigated from a new viewpoint. This time the work was done chiefly in America, at the Bureau of Soils in Washington, under the leadership of Milton Whitney. The theory of toxic substances in the soil as a cause of a lack of fertility was being advanced through the studies of Schreiner, Skinner and Shorey from the chemical standpoint, and by Livington from the physiological angle. To this body of work belongs also Cameron's study of the soil solution. This problem still remains in the region of debate, and is likely to receive further study.

MINERAL NUTRITION

The work on mineral nutrition, started in the laboratory of Sachs when he was a young man, advanced but little after his time. Of course, Knop's and Pfeffer's solutions and other salt balances had been used and the theory developed that only a small and definite number of inorganic constituents were required for the successful production of green plants. The function of the different elements was surmised in a general way. Potassium and nitrogen were associated with the increase in volume; iron was known to be necessary for chlorophyll formation, and the presence of magnesium in the chlorophyll molecule had been demonstrated by Willstätter.

The great influence of calcium on cell permeability and on the absorption of other ions of the nutrient medium was being investigated by the use of conductivity methods, first in America by True and Briggs and Bartlett and Osterhout, and in England by Stiles and Jergensen.

The main facts of toxicity and of antagonism were being studied by the same investigators following the pioneer work of Kahlenberg and True, through whose study the significance of the ion was shown to be general in the physiology of plants and of animals.

In another part of the field of plant physiology, the exact methods of the physicist were yielding important results in the studies of osmosis by Morse and his associates at Johns Hopkins, and by Berkeley and Hartley in England, and by Renner in Germany. The study of the lowering of the freezing point of plant saps by Dixon and Atkins was supplemented by the very intensive work carried on in America by Harris and his associates.

The very important work of Ursprung on suction tension was probably begun at this period, but did not come to full consideration until several years after the date of the present cross section.

WATER PHYSIOLOGY

The water question was receiving much attention. Chemically, a definitely important advance was made by the work of Babcock on the water of metabolism and its relation to the processes of nutrition. The water requirements of plants were being studied effectively and extensively by Livingston and by Briggs and Shantz. Out of these studies came light on wilting and other consequences of water shortage. The question of the course of water up the stem and out through the leaves was being approached from several angles. Renner published on the physics of transpiration in desert plants, while Lloyd was investigating the relation of stomatal movements to the problem. Sir Francis Darwin was contributing to the study of methods. The veteran Schwendender made what was perhaps his last contribution to plant physiology in a paper on transpiration. The work of H. H. Dixon seems to have done much to co-ordinate the various facts known regarding the ascent of sap and the process of transpiration. It seems likely, however, that this is not a final statement. Hasselbring, a little later, was investigating the relation of salt absorption to transpiration.

PROTEINS

The deeper things of plant nutrition were being attacked from the chemical vantage ground furnished by the fundamental work of Emil Fischer on protein chemistry that had just preceded our period. The work by Fischer was most effectively followed up by his student Abderhalden in his studies on the animal side of the problem. The study of vegetable proteins was being advanced notably in America by Thomas Osborne.

Asparagin physiology was being studied in Russia by Butkewitsch and by Prianischnikow and his co-workers. Walters, Krasnoselsky, Maximow, and others, followed the earlier work of Treub, whose chief contribution was an attempt to relate HCN to protein formation.

LIPOIDS

Perhaps here should be mentioned the subject of lipoid physiology, developed in this period chiefly by Ernst Overton, Bang, Palladin, Rosenbloom and others.

ADVANCES IN IRRITABILITY

During the past twenty-five years the relations of plant physiology to chemistry have multiplied and expanded until now a textbook on this subject would show little space devoted to other aspects of the subject, including irritability. This fact is perhaps due to the tremendous progress that chemistry has made during this period in such ways as have furnished methods available in the exact investigation of physiological problems. There has been no corresponding advance in methods of studying irritability. However, one conspicuous advance should be noted in this field. In the absence of anything more definite the transmission of stimuli has been assigned to the mysterious conducting powers of living protoplasm, it being perhaps assumed that something like a rudimentary nerve action might be here involved. However, the earlier work of Julius von Sachs contained the germ of later developments. In his assumption of organ-forming substances, he laid the basis for the hormone theory. This has been developed by Went and other investigators, chiefly Dutch, into a very interesting and fairly satisfactory explanation of stimulus conduction. Whether in other works of the early masters fertile germs still persist which may develop in this field, can hardly be foretold.

Turning toward the outlook for future development in plant physiology, the prospect for another era of progress seems bright. This opinion is based on the great advances being made by physics in the study of aspects of energy revealed in the recent work of physicists, chemists and astronomers. What the quantum theory may mean to plant physiology, as physiologists get into working relations with it, remains to be seen. Perhaps as work in energetics goes further, the old suggestion of Arthus may be found to have something of a basis. He contended that enzymes owe their marvelous ability, not to their chemical nature, but to the way in which the material is energized.

One of the greatest gains of plant physiology is the growing recognition that almost imponderable quantities of certain substances are found to have a very great influence on plant life. It seems likely that the ideal culture solution will eventually contain not merely the seven ions conventionally supposed to be necessary, but also a host of others in minute traces that in their own peculiar and fitting way influence the process of life. This great effectiveness of imponderables calls loudly for methods of determining the presence of substances in minute traces. Perhaps the magneto-optical analytical

So far as evidence goes fossil botany finds a very very close relation to botany because so many ancient types may be studied structurally, and the old landscapes may so often be visualized with much of beauty and accuracy. Witness the unsurpassed transparencies of the landscapes of geologic time in this garden as due to the artistic talent of Miss Purdy. Yet because fossil plants are so often found as indistinct imprints with leaf stem and fruit dissociated if preserved at all, their study has had to wait exceptional finds to a far greater extent than in the case of the vertebrates and invertebrates that make up such great displays as those of the American Museum of Natural History and the United States National Museum.

In short the fossil botanist must go where the evidence is to be found. But when he gets the evidence it is seen to be wonderful, and his subject is found to be in the fullest sense a world subject extending back and back in geologic time to the earliest of land plants of 500,000,000 years ago. It is indeed very interesting to me to recall Halley's comet again as I saw it while rounding Cape Hatteras on my way back from Mexico where I had just finished a course of field work on the mid-Mesozoic plants of the state of Oaxaca. There I measured up the first Liasic section for North America, and proved a far extended parallel with the remarkable cycadeoid floras of the Yorkshire coast and India. The results of this work were brought out in 1916 in quarto form with a fine series of plates printed at Frankfurt am Main, showing the presence of a rich and varied cycadeous vegetation.

Moreover it was about this time that Hamshaw Thomas of Cambridge was able to reconstruct the small flowered and freely branched cycadeoid *Williamsoniella* of the Yorkshire coast as seen to be closely related to the Rhaetic *Wielandiella* of Skone earlier studied by Nathorst. With all the new material and new facts in view it could no longer escape any one that the Mesozoic was not as so long supposed an age of cone-bearing cycads and of conifers, but an age of cycadeoids and therefore of flowering plants. For the first time the Mesozoic landscapes and forest canopies looked alive, vivid, understandable. Before, geologists had blandly asserted that the higher plants, the now dominant flowering plants, had suddenly appeared in the Cretaceous, albeit with little regard to simpler types of leaves and the ordinary arithmetic of fossil preservation and occurrence. But, as it were, in a few short years of productive research in laboratory and field it was now seen that flowering plants, angiosperms, might have had their clear beginnings as far back as Permian and even Carboniferous time. No less with these many new types in view, more and more difficult questions are put to the fossil botanist every day, and it is a very safe guess that he'll do extremely well if he succeeds in more satisfactorily reconstructing the ancient forest canopies in a truly satis-

fying detail with a full attention to plant succession and the approximate evolutionary sequence in time for the next appearance of the comet of Halley, or fifty years from now.

At no time has fossil botany enlisted a large number of workers such as pursue even some of the branches of botany, or even such a live subject as the fossil history of the vertebrates. But the past twenty-five years have proven wonderfully rich in results because of outright discovery, and especially improvement in methods of study for both the petrified materials and the carbonized imprints. It was a brighter day for fossil botany when A. G. Nathorst of Stockholm began thinking of severer study of the older northern floras by means of chemically cleaned surfaces and films. Other workers soon followed with improvement or extensions of the "chemical method" as Nathorst preferred to call it so that now it is widely applied to imprints, and along with etching and so-called "gelatine pulls" helps much in study of petrifactions. Notable extensions of these methods were used by Hollick and Jeffrey in their study of lignitized conifers, and also by R. E. Torrey in his fine demonstrations of types in American Cretaceous and Tertiary lignitized forests.

With then, improved method and finds afield, a comparatively small group of students has exactly during the past twenty-five years brought the lore of fossil plants into the form of a great subject. No botanist would now attempt to deal with problems of descent without the most careful consideration of the types of the past as now known in a clear enough general perspective to indicate at least the greater outlines of plant evolution. We have too the advantage of yet more and more extensive textbooks. There is the Fossil Plants of Seward in four volumes as followed by his fine account of Plant Life through the ages four years ago. We have the Paleobotanic handbook of Hirmer of 1927. Scott's splendid "Studies in Fossil Botany" have gone through further editions. It will be recalled that as they first appeared they belonged to the second twenty-five year period back as signalized by its great attack on the fossil botany of the Paleozoic by way of the "coal balls." Also, the delightful series of Aberystwith lectures by Scott appeared in 1924 as "Extinct Plants and Problems of Evolution." Even as readable a book is the "Plants of the Past" by Knowlton which appeared in 1927. Giving more attention to the Angiosperms this work distinctly supplements the Scott lectures.

Nextly there is to mention not only the catalogs of the British Museum but especially the Knowlton "Catalog of Mesozoic Plants" of 1919, so invaluable to any one who reads a text. There is also "Lehrbuch der Paläeobotanik" of Potonié as reissued in 1921 by Gothan in extremely well done

enlarged and up to date form. Of handbook extent are the Cycad-Conifer studies of Florin as mostly based on the fossil collections and the most elaborate consideration of leaf and stomatal features. Moreover textbooks on botany now frequently give much consideration to the fossils, notably Chamberlain's bright new text "Gymnosperms, Structure and Evolution," which has just appeared. We mention too Gager's "Fundamentals of Botany."

To list all the special studies and memoirs on the fossil plants of the past twenty-five years would mean more of formality than is here required. But any one must admit that the accounts of the most primitive of vascular plants as described by Kidston and Lang from the middle old red sandstone of Rhynie, Scotland, in the series of papers, 1917–1921 are remarkable alike for the types brought to light and their fine illustration. They are supplemented too by the accounts of Devonian plants by Kraeusel and Weyland again so finely illustrated that it is no longer true at all that on reaching the Devonian we "quit the dry land and put out to sea," as Hugh Miller said. Moreover in this country through the field study and collection of Loren C. Petry in the Devonian Genundewa limestone of the Finger Lake region of the state of New York an extremely fine series of the Callixylons of the Cordaite alliance has come to light. These have been studied by C. A. Arnold, and he has added accounts of the general type as seen in the large petrified logs of Indiana. Also E. M. Kindle has just now called my attention to the Indiana type *Callixylon Oweni* as recurring in uncommonly handsome preservation to the east of Lake Huron. The restoration of Gilboa forest at the State Hall, Albany, New York, by Miss Goldring, is splendid.

Leaving many other contributions by the wayside and coming down through the ages there flashes into view that wonderful find of Hamshaw Thomas in the "Gristhorpe beds" of the Yorkshire coast, Middle Estuarine shales and sandstones, between the Millepore Oölite and the Scarborough gray limestone, of mid-Jurassic age. There along the Cayton bay occurs the curious angiosperm *Caytonia,* one of the oldest of its kind yet seen, and both from form and the fine methods used in discovery promising many another unexpected or unpictured find in the course of the years. The type is again seen in the Jurassic of Greenland as determined by T. M. Harris who like Thomas and Florin has added much to our knowledge of the general features and character of Mesozoic vegetation as based on the study of the carbonized imprints.

In this country the field work of Noé on the coal balls of the mid-West is of outstanding interest and importance. The existence of such materials in our terranes seemed not to be known, through some strange oversight of

study. But much has been learned about them by now, and several interesting studies of the chemistry of coal ball petrifaction have also appeared.

Through the Carnegie Institution, Chaney and others have begun some very elaborate studies of Tertiary vegetation along the Pacific coastal region, with also examination of Mesozoic and Tertiary terranes in the Chinese region. But all the recent Tertiary studies cannot be noted with enough of care in short space.

It will be noted that I omit more direct mention of a considerable number of European contributions of a high importance—those of Bertrand, W. J. Jongmans, Renier, Max Hirmer, Edith Simson Scharold, Emily Dix, Susanne LeClerc, on the Carboniferous, and many others. Of interest and use is the " Microscopical Examination of Coal " by Clarence A. Seyler. There is also a rich addition to our knowledge of the seed ferns in Halle's study of Chinese types. While from India comes the varied studies of Sahni.

It is very easy to mention outstandingly interesting fields in fossil botany which have been neglected during the past twenty-five years—the Jurassic of Mexico, the Rhaetic of Argentina for instance, to say nothing of our own Virginia and North Carolina Rhaetic! There is also a question whether botanists use the fossil plants as much as they might in their direct illustration of botanical structure, that is in the everyday teaching of botany. The fossils allow great illustration, and can be so used as to greatly help the student to see and remember.

But the greatest advance of all to which we look forward as botanists and students of both the present and past as each illustrating the other, and even aiding the human mind to in some degree penetrate the future, is the establishment of field stations in connection with forestry and our series of parks and monuments. The possibilities of education and well-being are here beyond anything we can now see or easily predict. There can be no doubt but that the teaching values are of the highest. The time must come when we may all become better animals because more normal in our lives and better understanding the use of leisure. Always the fundamentals of knowledge and of science as the basis of a rational, human life will be in a manner hard to attain, will require industry, attention, purpose. But that initial effort once made the greater results for the individual must ever depend on the wisdom with which society, as organized and exemplified in our Federal Government uses the national resources in land and forests and mines.

The subject is too great, too far-reaching to go into to any extent. But the principles are fast reaching an understanding attention. Our national forests, parks and monuments have an untold value. They are only in their begin-

nings. They bear on adult education. Every one of them has the value of a collegiate institution, even a university in some special field.

Among our National monuments are three as yet somewhat unique, but for their kind surely destined to a great extension. These are the Dinosaur National Monument of Utah, The Arizona Petrified Forests of Adamana and Holbrook, and the Fossil Cycad National Monument of the Southern Black Hills as already mentioned. This brings us back to our subject again—the accomplishments of these twenty-five years, for our closing word, the FOSSIL CYCAD NATIONAL MONUMENT, its development.

When to take up an educational subject of deepest interest must depend firstly on available funds, and those funds must certainly in turn depend on the wealth of a country and the thrift and intelligence of its citizens. In our own country, accordingly, we find it difficult to believe that when it comes to sheer realities, the things that are surely worth while as seen through the years, we may claim either poverty, or the inability to act. Or in other words if we fail to do the fine things we'll find ourselves much poorer. Therefore I urge that the Department of Parks and Monuments neither lose nor delay a single further hour in the development of the FOSSIL CYCAD NATIONAL MONUMENT. Delayed eighteen post-wartime years, there not a dollar should be wasted, and not a dollar should be spared. I have estimated that adequate excavation on the cycad level, followed by development of material, and its housing in a field Museum, a scientific shrine, built in utter simplicity and taste to stand a thousand long years, may cost $65,000. The plan would fixedly be to house and to illustrate and display only the material *in situ,* so as to reach a sheer poetic simplicity, avoiding in every way mere advertisement, which ever tends to the general, the mediocre, the nondescript. That threefold significance, geologic, chemic, and biologic is enough. That which is surpassing needs no poor words of ours. All we might say is that there would be reproduced in its actual surroundings a landscape of the past which would again become green and move with life as it did so far back in dinosaur times. It would rest the eye of the mere sightseer, and that fadeless gemstone beauty would come into the life of every pupil of the schools, every student of botany down through the centuries. Such values must be well-nigh incalculable.

In this association we have urged on the attention of the Argentine administration the need for setting aside the second of the two finest petrified forests of the western world, the conifer forest of the Cerro Cuadrado in north central Patagonia as just now brought to exacter scientific notice. Such a forest should be kept intact and safe for the future. There is truth—all that a troubled world may hope for.

In no brief pages can all be told of the FOSSIL BOTANY of the period now discussed. But to such general survey as the foregoing a little of the particular may well be appended. Of much import is the free flowering feature of the cycadeoids as illustrated by the Mesaverde group of three species from the San Juan Basin of Northwestern New Mexico and Arizona secured in the years 1928–29 and since. Transverse (that is tangent) sections through the armor of old frond bases are shown for two of the species in the line

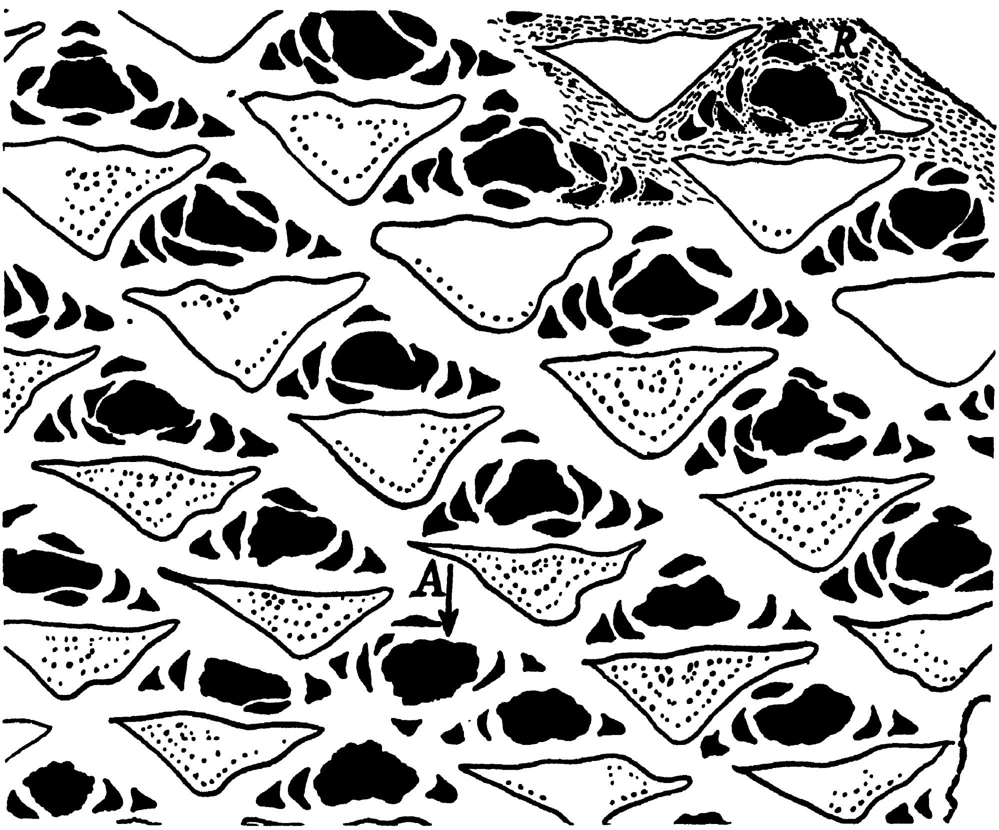


FIG. 1. *Monanthesia magnifica.* Mesaverde Cretaceous of the San Juan Basin, New Mexico. Transverse section through armor of old frond bases showing complete complement of axillary flower stalks with their bract husk as at A. The heavy mass of ramentum or chaff is indicated as at R. About natural size.

drawings, text figures 1, 2. The presence of a flower stalk or peduncle in the axilla of every old frond base of the spiral sequence is at once noted. Aside from slight variation in the frond base bundle pattern these species differ but little, going to make up with a third species (*Monanthesia aequalis*) a strikingly homogeneous group.

A further word too on the FOSSIL CYCAD NATIONAL MONUMENT as belonging so distinctly to our twenty five years is now possible to give. Aided during the past November by a group of CCC boys considerable excavation was carried out on the Monument front, proving at last indubitably that a rich store of material is yet present at this now historic and unrivalled locality. A splendid series of *in situ* specimens of varied specific feature from types with very small frond bases like *Cycadeoidea protea* up to the larger flowering forms like *Cycadeoidea dacotensis* and *Cycadeoidea colossalis* was

FIG. 2. *Monanthesia blanca*. Same general type and locality as the preceding species of Fig. 1. Some difference in the frond base bundle pattern may be noted, and in this species the foliage has been found.

brought to light in the course of the excavation. Unweathered, striking of form, varied of feature vegetative and floral, this rich display series from the monument itself will assure value and beauty to the Field Museum in which it is to be housed, construction at some time being now assured.

Answering the question of why such a display should be made, it is only needed to point out that as set where Nature indicated so many millions of

years ago, it will have a three-fold value—STRATIGRAPHIC, CHEMICAL, BIOLOGIC. In the very midst of the stratigraphic details of the Black Hills Lower Cretaceous, with the chemistry of petrifaction shown in the finest American petrified forest, student and tourist must alike get those genuine values easily that would come only with much labor if sought out in a city or average educational museum. Accessibility and true scenic beauty, as well as nearness to many other points of interest, add a last word of emphasis.

In Plate I is shown the south front of the Mesa lying but little above the cycadeoid yielding stratum. To the right of the row of pines is a very slightly faulted down slope along where so many specimens were eroded out originally. The chances are that more are yet present than have been hitherto collected all told. To the left in this view of Pl. I, forward at (x) is the point where the great branched trunk *Cycadeoidea superba* was secured yet *in situ* in undisturbed position clearly above the lesser line of slip and fault along the mesa front.

In Plate II is shown the north boundary of the Monument looking east. Entrance to the Monument will be from the valley (Chilson Cañón) seen in the right foreground. Even these briefly told views must give some idea of this intrinsically valuable NATIONAL MONUMENT.

PLATE I. FOSSIL CYCAD NATIONAL MONUMENT. Lower Cretaceous, Southern Black Hills Rim north of Edgmont, South Dakota. All of the foreground is in the petrified cycad-yielding terrane. To right of pines a zone of slip and slight faulting down. At X point where the splendid *Cycadeoidea superba* type was found in undisturbed *in situ* position.

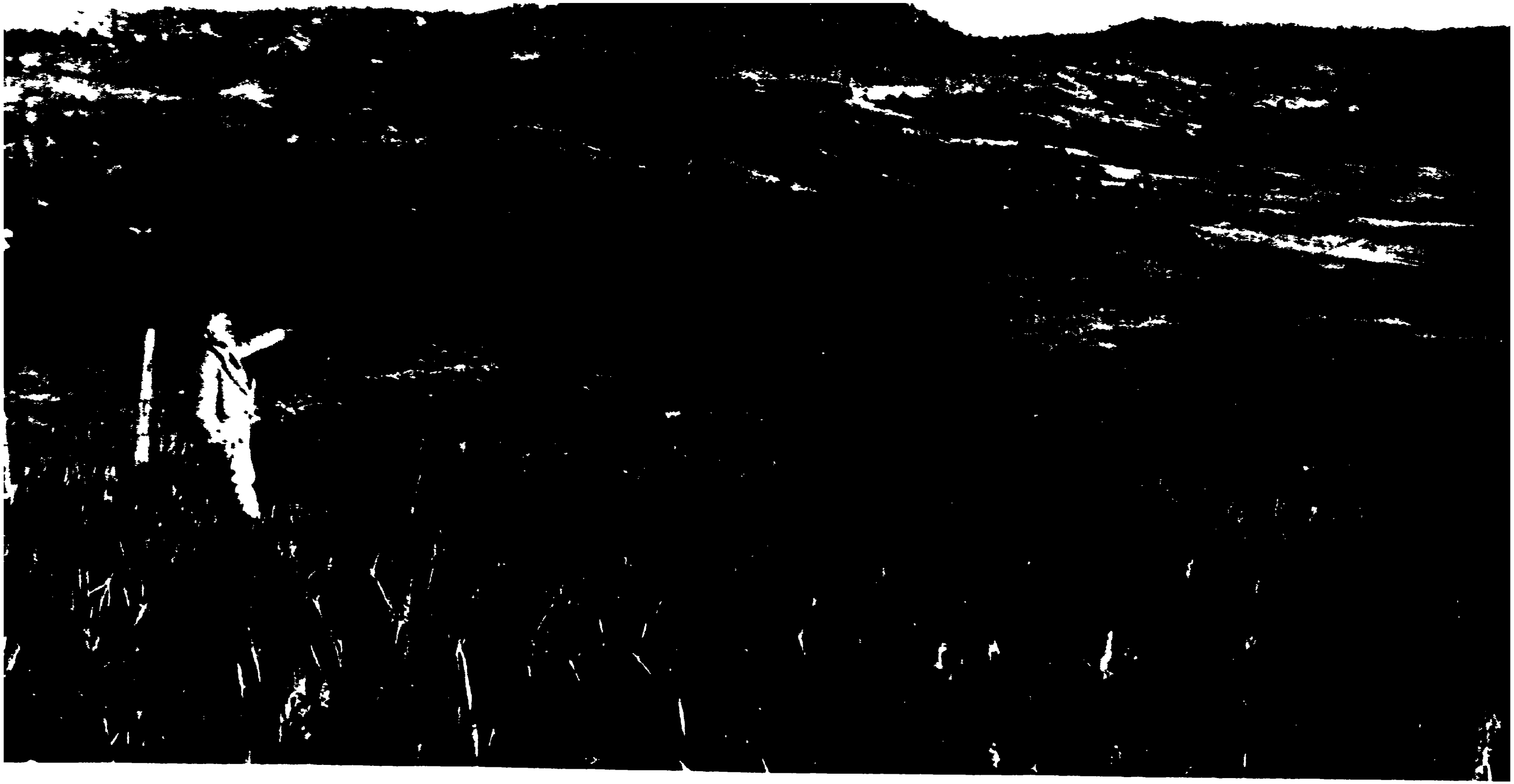
PLATE II. FOSSIL CYCAD NATIONAL MONUMENT. View along North boundary looking easterly toward point of entrance near Chilson Cañón, seen in right background. The bold mesa in the distance is formed by a quartzitic cap in the so-called Dakota sandstone which is the first member of the Upper Cretaceous.

The cycadeoids occur at the base of a sandstone much iron stained, capping a thirty foot shale horizon which comes in about one hundred feet above the marine Jura. The cycadeoids are thus not higher up than Lowermost Lower Cretaceous. Both these views show the Monument to be in the very center of some of the most interesting geology and stratigraphy in the Northwest.

PLATE I

WIELAND—FOSSIL CYCAD NATIONAL MONUMENT

PLATE II



WIELAND—FOSSIL CYCAD NATIONAL MONUMENT.

PLANT PATENTS

Robert Starr Allyn

Deputy Commissioner of Sanitation, New York City

The subject of Plant Patents is very important and well worth your careful study but on account of the brief time allowed I can say but little as to the various technical and controversial features of the law and Patent Office practice.

It doubtless will interest you to know that when the bill to provide for Plant Patents was before Congress in 1930 the only person in the Senate or House who apparently appreciated the difficulties involved was the gentleman who is now the Mayor of New York, the Honorable Fiorella H. LaGuardia. The evidence of this will be found in the Congressional Record.

You are probably all generally familiar with the fact that we have a so-called " Patent System," and that it has been an important factor in the development of our resources.

Provision was made for it in the Constitution which states:

> " The Congress shall have power . . . to promote the progress of science and useful arts, by securing for limited times to authors and inventors the exclusive right to their respective writings and discoveries."

Authors of art, books and music and inventors of machines, products and processes have accordingly been rewarded for their contributions by copyrights and patents. Just why our patent laws have not (until 1930) provided for rewards to those who have created (with nature's aid) new plants we do not know.

In an article on the " Making of a Plant Hybrid," Dr. David Fairchild, president of the American Genetic Association, described in *The Journal of Heredity*, in February 1927, in great detail the crossing of an *Actinidia Arguta* (Japanese Kokuwa) with an *Actinidia Chinensis* (" Yang Tao "). This was more than three years before the passage of the Plant Patent Act, but Dr. Fairchild in discussing the commercial possibilities of his new fruit said:

> " But all these things must remain still in the lap of the gods! The hybrid is made; let it take its course. It shall have to, since the Patent Laws of America will give me no assistance. Were they fair and designed to support

invention in other fields than in those of mechanical things, and did they fulfill the objects laid down in the Constitution, matters might be quite otherwise and I might awake some day, as inventors have, to find myself drawing a royalty from my Actinidia Hybrid. Let us hope that some day conditions can be changed so that plant breeders, who are adding countless billions to the wealth of the world, may receive something more substantial than the casual recognition which people generally accord to those who give them something for nothing."

On February 11th, 1930, identical bills were simultaneously introduced in the Senate by Hon. John G. Townsend, Jr., of Delaware (S. 3530) and in the House of Representatives by Hon. Fred S. Purnell, of Indiana (H. R. 9765). These bills were referred to the respective committees on patents in the Senate and House, and to the Secretaries of Agriculture and of Commerce. The proposal was to grant patents on:

"Any new and distinct *variety* of *asexually* reproduced PLANT *other than* a tuber propagated plant or a plant which reproduces itself without human aid,"

and that

"The words invented and discovered as used in this section, in regard to asexually reproduced plants, shall be interpreted to include invention and discovery in the sense of *finding* a thing already existing and reproducing the same as well as in the sense of creating."

The Committee on Patents reported:

"The purpose of the bill is to afford agriculture, so far as practicable, the same opportunity to participate in the benefits of the patent system as has been given industry, and thus assist in placing agriculture on a basis of economic equality with industry. The bill will remove the existing discrimination between plant developers and industrial inventors. To these ends the bill provides that any person who invents or discovers a new and distinct variety of plant shall be given by patent an exclusive right to propagate that plant by asexual reproduction; that is, by grafting, budding, cuttings, layering, division, and the like, but not by seeds. The bill does not provide for patents upon varieties of plants newly found by plant explorers or others, growing in an uncultivated or wild state.

"It is hoped that the bill will afford a sound basis for investing capital in plant breeding and consequently stimulate plant development through private funds."

The bills with amendments were passed by both Houses of Congress and became a law on May 23, 1930 by the approval of President Hoover.

I might add that *the law does not give any right to propagate plants,* but merely the right to prevent others from making, using, selling, or asexually reproducing the patented plant.

In my opinion the bills were unduly hastened through Congress, and are inadequate properly to reward plant breeders and to protect horticulturists as well as florists.

However, we now have a law intended to reward the " inventor " of those distinct and new plants which have been asexually reproduced. Doubtless it will be amended to adequately reward *discoveries* of other new plants and their *products.* It should be noted that the *present* law relates solely to *plants* and not to seeds, flowers, or fruits. Unfortunately the Patent Office has overlooked this feature of the law in several cases, and has pretended to grant patents on a strawberry *per se,* a pecan, a grape-fruit, *an apple,* and various flowers—the fruits or flowers as distinct from the plants.

The person who is responsible for the production of the asexually reproduced new plant is the *inventor* and may apply for the patent. He may or may not know what he has done to bring forth the new feature, but in my opinion he must have performed some act in addition to merely finding or observing the novel plant.

The Patent Office seems to regard a *newly found* plant as patentable if found by a *professional* plant explorer or breeder but there is nothing in the law upon which to base this distinction. Plant inventions may be kept for the personal satisfaction of the breeder or assigned to others.

In the case of developments made in connection with Agricultural Experiment Stations and Botanic Gardens it is most appropriate that they be assigned to the organization which finances the work.

If you have ethical scruples against personal profit you might transfer your rights to the Brooklyn Institute of Arts and Sciences, Inc., for the benefit of the Botanic Garden.

The Blake Peach patent No. 31 was assigned to the New Jersey State Agricultural Experiment Station.

The Pring Water Lily No. 55 was issued to the Missouri Botanical Garden.

I might add that Soviet Russia has found it necessary to provide for the Grant of Patents in order to encourage progress.

The application for a U. S. Plant patent is examined as to form by the Patent Office Examiner and as to novelty by the Bureau of Plant Industry in the Department of Agriculture and it takes approximately a year to get a patent.

Thus far there have been about 125 Plant Patents issued and we will show examples on the screen of some 30 or 40 flowers, fruits and nuts. It is of interest to note that more than 2,000,000 other U. S. Patents have been issued.

The novelty in many cases is not at all apparent. Possibly a chromosome study would satisfy some of you. Some of the colors are very beautiful, as you will see.

In order to satisfy the intent of the Constitution, of course, the new plant *should* represent "progress." The intent of Congress in 1930 was that the new characteristics should be distinct but they must have had a premonition of the events to come, for the Committee report said:

> "it is immaterial whether in the judgment of the Patent Office the new characteristics are inferior or superior to those of existing varieties. Experience has shown the absurdity of many views held as to the value of new varieties at the time of their creation."

It may be, in fact, that it will be regarded as an advantage to produce smaller plants—fruits that will not keep—flowers that quickly fade—trees that are susceptible to decay—plants that readily succumb to disease.

Thus far the most common distinguishing features of the new plants have been the shape of the flowers, the vigor of the plants, the increased productiveness, the size of flowers, the earlier or later ripening period of the fruit, unique foliage, the fragrance of the flowers, everblooming habits, and resistance to disease.

The greatest number of new plants have come from California (28), Indiana (10) and New York (8), with a scattering from some other states. There have been 15 foreign roses and 2 foreign freesias. It is of interest to note that in 1933 the first Plant Patent was issued in Germany (No. 582,983) on a fruit tree improved as to the root portions. So far as I know, no other country rewards Plant Breeders by issuing patents.

I think that the only new plants originating in New York State are 7 roses and one violet.

California gets credit for 9 Burbank patents on plums, a peach, a cherry and roses, although Luther Burbank died in 1926.

I have been surprised to find only six women inventors, four of whom have contributed new roses, one an avocado, and one a plum.

The Secretary of the : terior, Mr. H. L. Ickes, has produced a new Dahlia, named after his wife.

The slides were made by Mr. Louis Buhle of the Brooklyn Botanic Gar-

den, and colored by Miss Elizabeth Bonta. The following abstracts are of interest in connection with the exhibition of the slides.

1. Climbing Rose.
Improvement on " Dr. Van Fleet."
Called the " New Dawn."
Everblooming characteristic.
2. Rose.
Cross from the General Jacqueminot and the Richmond rose.
Called " Rose Senior."
Scarlet crimson outer petal, cordate shape.
3. Carnation.
Found as a sport on a plant of pink *Sophelia,* March 1, 1929.
Called " Joan Marie."
Large size, white, flecked with pink, etc.
4. Thornless Young Dewberry.
Discovered as a sport in a field of " Young " dewberries in Chico, California, in 1928. (Published in the *Journal of Heredity* for December 1929.)
Called " Thornless Young Dewberry."
Absence of thorns.
10. Climbing rose.
Cross between Paul's Scarlet Climber and Gruss an Teplitz.
Called " Blaze."
Everblooming.
14. Plum.
No mention of origin.
Early ripening period.
17. Freesia.
Parentage is obscure.
Called " Elder's Giant White."
Giant waxy white—large number of corms.
19. Dahlia.
Cross between the " Jersey's Beauty " and the " Mrs. I. deVer Warner."
Called " Anna W. Ickes."
Coral red—shape of petals.
20. Yellow Rose.
Sport of the Talisman.
Rich golden color—shape of flowers.

21. Cerise Rose.
Hybrid Tea Rose.
Deep cerise, fragrance, strong stems, prolific.

27. Mushroom.
No history.
Called " Golden White."
White cap, floccose scales oxidizing to pale buff.

29. Cherry.
Bud sport of Montmorency.
Called " Eveline."
Late ripening.

30. Cherry.
Apparently a bud sport of Montmorency.
Called " Jordan."
Early ripening.

43. Freesia.
Cross of *Freesia refracta alba* and *Freesia* yellow major.
Called " Joan Manda " or " Lily flowered freesia."
Shape of large white blossoms.

46. Strawberry.
Cross between Premier or Howard 17 and Gandy.
Called " Jupiter."
Heavy plant growth, early ripening, color, shape and flavor.

49. Hybrid Tea Rose.
Originated as a sport of the rose Grillodale.
Called " American Pride."
White and pink—shape.

53. Colored Seedless Grapefruit.
Original was found in 1929 on a " Thompson Pink."
Called " Henninger Ruby."
Pink and seedless.

54. Evergreen Plant.
Originated as a seedling probably of *Juniperus communis.*
Wide leaves, dark green below and blue on top.

55. Water Lily.
Claimed as the descendant of *Nymphaea,* Mrs. George H. Pring and *N. Stuhlmannii.*
Called " Saint Louis."
Yellow tropical day lily.

57. Apple Tree.
Discovered as a sport upon a Stayman winesap.
Early red color before ripening.

58. Chrysanthemum.
Third generation hybrid.
Nopal red to ox blood.

59. Hybrid Tea Rose.
Talisman sport " discovered."
Called " Red Talisman."
Carmine buds—pink shading and novel shape.

65. Rose.
Apparently a hybrid of *Rosa rugosa* and *Rosa multiflora.*
Called " Apple Blossom."
Rambler—cluster—color and form.

67. Hybrid Tea Rose.
Cross between a Premier Supreme and a McGredy's Scarlet.
Called " Mrs. J. D. Eisele."
Red—vigorous—productive—camellia form.

68. Snapdragon.
No indication of origin.
Called " Afterglow."
Double blossoms.

70. Rose.
Cross between a Veilchenblau and blue sport of same variety.
Extraordinary growth of wood.

73. Pecan Tree.
" Discovered " in 1927 when about 15 years old.
Called " Humble " pecan.
Vigorous growth, distinctive shell and stems.

74. Apricot.
No indication of parentage.
Early ripening, attractive color and excellent flavor.

77. Gladiolus.
Believed produced from cross pollination of " Golden Dream " and an unnamed yellow variety.
Large sized buds, perfect form, yellow color.

79. Rose.
Cross between a Frau Karl Druschki and a Souvenir de Claudius Pernet.

Called " Weigand's Pink Druschki."
Flesh pink color, fragrant odor, profuse bloom.

82. Thornless Logan Blackberry.
Sport discovered in San Gabriel, California.
Heavy growth—no thorns, large berries.

83. Viola.
Originated as a seedling, one parent a Jersey Gem and other unknown.
Small, compact foliage, large flowers, fragrant odor, strong plant.

87. Rose.
Originated in Hasloh, Germany.
Called " Nigrette."
Nearly black rose—persistent color.

88. Seedless Grape.
Called " Sultan."
Special growth, leaves, clusters. Petiolar sinus.—U-shaped.

89. Pendulous *Juniperus Scopulorum.*
Wild tree found in canyon in northern New Mexico.
Slender pendulous branches.

93. Gardenia Plant.
Giant—white—vigorous growth.

99. Hybrid Barberry.
Cross between *Berberis thunbergi* and *Berberis juliana.*
Hardy growth—free from rust.

100. Avocado.
Parentage unknown.
Green colored—pear shaped—summer ripening.

107. Rose.
Sport of Else Poulsen.
Wavy fluted petals, contrasting colors.

113. Raspberry.
No mention of origin.
Light colored plant, strong canes, free from briars, cream colored light pink berries.

118. Phlox.
Discovery—chance seedling.
Dark green foliage, abundance of bloom heads, pastel pink.

119. Mango.
Cross between " Cecil " and either Mulgoba or Haden.
Low and vigorous growth, numerable crops, freedom from fibre of fruit.

Quite a number of these new plants are on the market at prices above those of similar unpatented plants.

I am sorry that time has not permitted a more complete discussion and showing of others of these new features. I hope, however, you will think about the subject and endeavor to profit by the new law.

OPPORTUNITIES FOR WOMEN IN HORTICULTURE, 1910–1935

Kate Barratt

Principal, The Swanley (England) Horticultural College

The professional woman gardener twenty-five years ago was a relatively rare phenomenon in England and her opportunities for work were very much restricted, being confined for the most part to the smaller private gardens. They shared with their sisters, who were endeavoring to make their way in other professions, in the general prejudice against the entry of women into spheres which had hitherto been monopolized by men. To-day all this has changed for the better; the war with its opportunities of service, so gladly embraced by women, showed that there were few fields in which capable women could not hold their own in coöperation with men.

Not only has there been a steady though not a striking increase in the number of women finding employment in horticulture, but the avenues have widened and opportunities are now available in almost every department in which men are normally employed.

In this connection it is pertinent to refer to the striking developments which have taken place in all branches of horticulture during the period under review. In fact it would be impossible to give a true picture of the improvement in the position of women in gardening without reference to the circumstances which have led up to it, and undoubtedly the most important are the changes in the industry itself. Of these perhaps the most interesting has been the growth of the wide popular interest in gardening which extends to all classes of the population.

There have always been cottage gardens in England, gay with old-fashioned flowers, beautiful in their haphazard arrangement of mass and color, but never in the past have the suburbs of the large cities been made so attractive by the cultivation of their gardens as they are at the present time, stimulated by London Gardens Guild.

The real love for plants of the British people and their pleasure in cultivating them has led to the world-wide search for new and interesting species and their introduction and acclimatisation. China, North India, Thibet, North America and South Africa have all yielded their treasures. These are not like so many of the earlier introductions, plants which require the resources of a heated conservatory or stove house for their successful culture, and

which were therefore grown in comparatively small numbers, but being natives of temperate or even cold climates are readily established in the English flower garden, and have wonderfully increased the beauty and variety of our gardens. The older type of carpet bedding, though it still finds its place in more formal gardens has been largely replaced by the irregular grouping and variety of form and color of the herbaceous border and wild garden.

I need not remind this audience how much the development of this side of gardening owes to the influence and inspiration of such women as Gertrude Gekyll and Ellen Willmott, whose recent loss we have had to mourn. It has appealed particularly to the owners of small gardens and has helped to swell the great army of amateurs who are keenly interested in the craft. There is direct evidence of this in the numerous active societies which devote themselves to the study of special groups of plants such as roses, lilies, alpines, iris, etc.

In all these activities women play their part both as amateurs and paid workers filling such positions as head and assistant gardeners, suppliers of nursery stock and advisors and designers of gardens.

In view of the notable achievement of English Landscape Gardeners in the past it must be difficult for American people to understand the relatively small part which landscape architecture has played in later times in England. This is in large measure due to the comparatively small field offered in the laying out of large estates and to the consequent absence of an active school of landscape gardening. Much of the planning of small gardens was undertaken by the nurseryman. There has been, however, in recent years an active development of interest in this subject largely inspired, I believe, by American example. The formation of garden cities, the adoption of schemes of town planning under Government auspices has provided the opportunity, and there has recently been formed in England an Institute of Landscape Architects whose influence has already been exerted both in the direction of protecting the status and work of the existing professional landscape architect, and in making provision for a more adequate training school.

This particular field of work offers congenial opportunities to the right women and one is glad to see them taking a helpful position in the van of the new movement.

Landscape architecture is an art, and gardening is first and foremost a craft, and it must be realized that the woman gardener in England is a craftswoman who is able to carrv out herself all the manual operations concerned with the growing of plants. I myself believe that only in this way can a real knowledge of the possibilities of the utilization of plants for decorative effect be fully realized, and the training in the craft of gardening is the surest

foundation on to which to build a knowledge of the art of landscape architecture.

The most significant development in horticulture in England during the period under review has been the growth of its commercial side, that is to say, the production of fruit, vegetables and flowers for market. This has been the result of many contributory causes, the war, which brought the realization of the importance of home-grown food, the political and financial troubles of recent years, which have given this further emphasis, the improvement in methods of cultivation and marketing and above all a gradual change in the dietetic habits and tastes of the people. Fresh fruit and salads now form an essential part of the diet of every household apart from the very poor. Much of the fruit consumed in Great Britain is still imported but it is highly significant that the acreage of fruit land in England has increased by 71,510 acres during the past twelve years, 23 per cent.

This remarkable development has been greatly assisted by the work of such research stations as East Malling in Kent, Long Ashton in Gloucestershire and Cheshunt in Hertfordshire, which have greatly reduced the inevitable elements of uncertainty and chance in production and are helping to establish the work of fruit growing on the orderly routine of a factory system; so far that is, as this is possible in any process in which the weather has the last and decisive word.

The growth of the industry has been promoted by reduced labor costs due to introduction of mechanical cultivation but still more to improvements both in the methods and standard of the marketing of fruit. Here I may pay a tribute to the example given by American practice and to the development of coöperative systems of grading, packing and storing of produce.

With our very large urban population the cut flower trade is becoming of increasing importance. Its value has been doubled in the last ten years and last year over 75,000,000 dollars were spent in England on the purchase of cut flowers.

In all these branches of commercial horticulture women are taking part, both as workers and as owner-managers, and indeed there is an excellent opening for them as growers of fruit, vegetables and flowers for market and particularly in the florist trade which is expanding very rapidly. The progressive measures already referred to are all to the advantage of the woman grower, and there would be many more engaged in the industry if they could command the necessary capital.

A word must be added as to the opportunities for the training open to women. The facilities for horticultural education available in England are good on the whole and women are particularly fortunate in this respect. The

two colleges for women only at Swanley in Kent and Studley in Warwickshire have had a respectably long history, the former which is the oldest and largest having been established 46 years ago, and they have led the way in shaping the course of horticultural education. Women as well as men are also admitted to the horticultural department of the University of Reading, as well as to some of the schools owned by local educational authorities.

The chief difficulty which women have always experienced on leaving college is that of obtaining subsequent varied experience, especially in the commercial branches. There is still a tendency to look on them with suspicion and to regard their value and abilities with some scepticism. This is no doubt a survival from the days, not long past, when " brawn " as well as brains was an essential part of the equipment of the successful grower.

In England the college trained girl is largely drawn from the middle class of society and the majority are the daughters of professional and business men anxious to take up a career which will give them opportunities of life in the open air away from the city. Generally they know little, if anything, of the subject when they enter the college from school, but it is seldom that they regret their choice. Their instinctive desire for an outdoor life can be fully satisfied by the opportunities offered in the world of horticulture.

Twenty-five years ago a considerable proportion of the students entering Swanley had sufficient private means to make them independent of any subsequent paid work, and the great majority paid the whole of the fees from their own resources. I have, however, in an experience extending over many years, been able to trace a slow but persistent change in the type of student joining the College. The increased opportunities for professional employment have recruited a larger proportion of girls and women who will be dependent on their own efforts for a livelihood, the growth of knowledge of scientific principles and their applications has attracted a more studious type of graduate, and a considerable proportion of these students require and receive financial aid to enable them to complete their training. At the present time about one third of the students are helped by grants from public sources.

The extent to which the training facilities are utilized is indicated by the average number of students at any one time in the various colleges. They number approximately 140–150, and of these about one half will be preparing for college diplomas or university degrees, that is to say, taking courses lasting at least three years.

I cannot close this paper without reference to another direction in which numerous women gardeners have found congenial employment. Even twenty-five years ago many were engaged in managing the gardens attached to some of our schools for girls (very few mixed schools in England). Dur-

ing the intervening years the standard of training of women gardeners in scientific principles has been steadily raised and this has been very much assisted by the establishment of degrees in Horticulture in the University of London and also in the University of Reading. As a result there are now available women graduates who are not only capable gardeners but who are well qualified to teach biology and to illustrate its principles by their garden practice. Others of these highly trained women are engaged in research, advisory work and other branches of horticultural education. At present the number of appointments held by women and the number of candidates for the positions is not large, but they are steadily increasing and I am certain that Miss Shaw would be very gratified with the progress made in the development of school gardening since her visit to England in 1931.

Though I am not concerned in tracing the growth of the gardening movement for women in any country but my own I may refer to the fact that our women's colleges have always attracted students from abroad, even from those few European countries in which gardening schools for women already exist. It may be interesting to record that most of the European students are drawn from the northern countries, Holland, Switzerland, Germany and Scandinavia.

In reviewing the position of women to-day in the world of horticulture it will be seen that it has undoubtedly improved with the general progress of the subject, but it is also one of those activities which appeals very strongly to the natural instincts of women, and therefore provides a satisfying hobby as well as a career. Indeed it is difficult to separate the two aspects for there are many with whom gardening was first adopted as a hobby and subsequently developed as a career under the stress of economic conditions. In either case its supreme advantage is its power to satisfy the innate desire possessed by many women for outdoor pursuits and the enjoyment of cultivating and caring for living things.

The ability of women to grow plants and to design gardens is accepted generally but the right of women to compete for paid positions is still too often conceded in theory only. On the other hand the commercial sphere is open to all who can find the capital to establish fruit orchards, market gardens or nurseries of their own. It is here that women should enter in greater numbers with a fixed determination to show that they can achieve an equal success in all branches.

At the beginning of this paper I said that the number of women engaged in gardening had shown a steady but not a striking increase in the past twenty-five years. This is true, despite the fact that a steady stream of trained young women have left the colleges during this period. We must not however forget

that there is another and overmastering call which draws women from their chosen profession to take another more important and more absorbing, that of marriage and motherhood. It is true that in building a home they do not sacrifice their garden activities, but subordinate them, *but* from our present standpoint most of them pass out of the profession and no longer count as active units in what must be described as the changing population of women gardeners.

GROWING PLANTS IN SAND WITH THE AID OF NUTRIENT SOLUTIONS: WITH SPECIAL REFERENCE TO PRACTICAL APPLICATIONS

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Modern methods of research with plants has brought about a rapid increase in our knowledge of the rôle that the various elements, especially minerals, play in the life and development of agricultural plants, and with these we include also horticultural plants. For example, it has long been known that potash is an essential element for all plants that manufacture and have special organs for the storage of carbohydrates, such as sugars and starches. Among these are sugar-beets, potatoes, corn, wheat and so on. The special significance, recently determined, is that nitrogen, which is essential for growth, cannot be assimilated unless potash is present. This means that a plant may exhibit symptoms of nitrogen starvation in the presence of considerable quantities of nitrogen, if potash is lacking.

Garden soil is a very complex body, made up of mineral and organic matter, variable in chemical and physical composition. It is many years since many plant physiologists and horticulturalists realized that research with plants in soil was not very satisfactory. Some other medium for the growing of plants was necessary. Sachs, 60 or so years ago, made use of sand as a substratum for the growing of plants, using solutions of chemicals. Many other investigators were more or less successful in the use of this method of growing plants. It was not until the time of the World War, however, that the most decided advance came. It appeared to be necessary to produce more food stuffs on a relatively limited amount of land, and so more must be known of the chemical processes in the life economy of the plant. Accordingly, under the National Research Council, a cooperative project was established throughout the country, chiefly in public research institutions, to inquire into the salt requirements of agricultural plants. Tottingham, Shive, and others evolved solutions containing three or four chemical salts which would grow plants satisfactorily either in water cultures or in sand cultures, except for a few sparingly utilized elements, such as manganese, boron, zinc, copper, and so on, of which only a trace is necessary. Technique was developed, not only in

the culture of the plants, but also in the analysis of plant tissue. Instead, for example, of analyzing plants for total nitrogen, the analysis for nitrogen is broken down into fractions, as nitrates, nitrites, ammonia, amino-acids, and so on. It was learned that these various forms of nitrogen would be found in plant issue of different stages of maturity.

These findings were made possible because of improved technique, by growing plants under conditions when the supply of mineral nütrients, which are absorbed through the roots, can be kept under absolute control; that is, by growing in sand or in water cultures. The sand which is used is free from organic matter, is washed until all soluble and easily suspended material is removed, so that nothing remains but grains of quartz among which the roots can penetrate and thus the plant will be supported.

In prosecuting an investigation with a certain plant, as for example the carnation, the first thing necessary is to find out what proportions of the salts used are necessary, because plants vary considerably in their requirements. In most of our work, we use a solution containing four salts: namely, calcium nitrate, monobasic potassium phosphate, ammonium sulfate and magnesium sulfate. These are used in a chemically pure state. First what is known as a triangle or polygon is laid out, in which each salt is represented as the side of a polygon. Such a series as laid out usually consists of 20 or more solutions. All solutions are made up in such a way that the osmotic concentration is one atmosphere, that is, there is a balance between the concentration of the plant sap and the external solution about the roots.

If the proportion of one salt is decreased, then one or all the other salts must be increased in order to maintain the concentration. These solutions are made with distilled water. The method of application used in this preliminary work is known as the "constant drip." A reservoir of suitable size is placed near each plant and thence, by means of a siphon made of capillary or thermometer tubing, the solution is carried to the sand in which the plant is growing. These siphons are adjusted to give a regular supply, usually one liter or about one quart, every twenty-four hours, drop by drop. By this means, the roots of the plants are continuously bathed by a fresh supply of the nutrient solution, and, at the same time, a fresh supply of air is carried into the sand to permit exchange of gases. In properly aerated sand or water cultures, the growth of roots is much greater than in a poorly aerated medium. The plants are usually carried in these cultures during the crop year, which may be three months or six months or more, some plants being cultured two years. In the meantime, however, certain of the solutions are seen to be unsuitable for the culture of that particular plant. Often these give very important information concerning the effect of excesses or deficiencies of certain

elements or combinations of elements upon the plant under investigation. As a result of this test, usually one or more solutions will be found that will produce satisfactory plants, and these solutions are used as a basis of further researches. With most plants, it is necessary to add to the solution traces of iron to prevent chlorosis or yellowing of the foliage, and sometimes traces of boron, manganese and some other minor elements.

After operating the triangle with carnations, the plants grew so well that there seemed to be commercial possibilities in the method. Accordingly, we set aside one section of greenhouse, 33 feet $\times$ 75 feet, containing five benches. These benches were divided into plots five feet long, which was done to give a number of replicates of any treatments. In the greenhouse test, there were compared the white washed sand that was used for the initial culture work, a yellow bank sand from the College Farm, and a composted soil suitable for growing carnations. The soil was handled as the commercial carnation grower would handle it, as to fertilizer and other practices.

We had faith enough to install in the attic over the greenhouse headhouse a wooden vat, which was connected with the water supply and from which pipes were carried into the carnation house, through which the solution would flow by gravity. The nutrient solution is now composed of salts that are not so refined as those used in the initial work, and tap water is used instead of distilled water.

The carnation plants had been growing in the field from the middle of April until July, when they were benched. The plants were lifted from the soil and all the soil was washed from the roots, after which they were benched.

After the growing season, we learned that the plants in sand produced just as many flowers as those in soil, and further that the production in sand was greater during the winter when prices were higher. The length of stems, the size and quality of the flowers and the keeping quality is just as good in sand as in soil. In addition, there were fewer flowers with split calyxes. There was less disease in sand than in soil. Further, the labor costs were far less. With the nutrients went on enough water to save labor of one watering operation. It was not necessary to till the sand, to kill weeds, and to work the fertilizer in, as is necessary with soil. Except in extremely hot weather, the sand did not require more frequent watering than the soil. This test has been repeated annually, and now all the carnations which we grow for commercial production are planted in sand. Further, some of the sand is now in its sixth year in the bench and there is no evidence that it is reduced in efficiency. The type of sand seemed to make no difference, but sand that has been washed, as is all sand for concrete, is to be preferred. Formerly, the practice had been to remove the soil annually and replace it with freshly com-

posted soil. This involves a great amount of labor, besides the difficulty in securing good soil and manure for composting.

The advantages in sand culture are chiefly economic. It appears that once the sand is in the benches, it may be a number of years before it will need to be replaced, and the period of usefulness will be lengthened by care in washing the roots before planting so as not to introduce fine soil material into the sand, and by digging the plants carefully at the end of the season so as not to leave too much of the root system. The cost of the nutrient salts is less than the cost of fertilizers and they can be mixed and applied by a man of ordinary intelligence. One watering operation is performed in the application of the nutrients. If the weather conditions are such that plants cannot utilize nutrients, they may be withheld or even washed out of the sand, while in soil, plants must take up nutrients whether they need them or not. If the plants in sand should become diseased, there is not much danger of the disease being carried over, and, if it should be, the sand can be saturated with a fungicide and germicide, such as bichloride of mercury, and this washed out again as soon as it has done its work.

In order to overcome objections to washing the soil from the roots before benching and also to learn a better means of carrying the plants continuously under glass, as is necessary in some parts of the country because of branch rot, a new technique is being developed. As soon as the cuttings are rooted, in December or January, they are potted up in sand in three-inch pots and are carried in these pots all summer. The heat retards development, so that they have not been quite as good as field grown plants. However, by midwinter they are as large and are producing as many flowers.

One practice that should not be neglected is flushing. At least once in two weeks, the sand should be thoroughly flushed. This is to get rid of excess salts and harmful residues left after the plants have taken what they can. This practice is especially necessary with roses, which soon show a chlorosis or yellowing of the leaves, as a result of these residues.

We have no hesitancy in recommending this method of carnation culture to anyone who desires to try it. One grower on a private estate has grown carnations for about four years in sand, and he stated that he would never go back to the soil again.

Roses have been grown successfully in benches, and one commercial grower, after trying the method on a small scale, has gradually expanded until he now has 1000 plants in and in ground beds and expects to increase this number gradually until all of his roses are under this type of culture. Snapdragons and gerberas are also being grown in sand. One test we are now making we call the "bath-tub." The bench is lined with a copper coated

paper. The solution is in a tank and is pumped into the sand by an automatic sump pump, the solution being used repeatedly. Snapdragons in this culture are growing and producing well.

Because of the ability to manipulate the solution some very interesting effects have been obtained. Sweet peas grown under glass have a serious fault in that the flower buds fail to open and drop off during mid-winter. Plants were grown in a triangle to determine the best solution. The following year, a group of plants were subjected to varying treatments. One group received a solution of one-half atmosphere concentration, or a solution twice as dilute as that ordinarily used. The plants made a tremendous vegetative growth; but when the dark days of winter set in, hardly a flower was produced, practically all of the buds dropping. Another group received nutrients of three atmospheres concentration, that is, three times as concentrated as normal. These grew slowly, but when winter came, they produced good flowers all during the season of dark weather. It will be possible to grow the plants with a dilute solution up to a certain point, producing good plants. Then the solution can be changed to the one of higher concentration, the growth will be checked and flowers will be produced.

Another plant that behaved in much the same manner is the poinsettia, and this is also an example of how the commercial grower can take advantage of this method. The plants were in 5 inch pots in sand, having a restricted root system. One plant received nutrients of one-half atmosphere concentration, and reached a height of more than four feet, the flower heads being 18 inches across. A second plant with normal concentration made about half that growth; while one with solutions of two atmospheres concentration was shorter with smaller flowers. These three plants were taken into my household three days before Christmas, and received no further nutrients except tap-water. Within two days the leaves began to yellow on the tallest plant, which received the one-half atmosphere concentration, and within three days the leaves and colored bracts began to fall. In about a week, two-thirds of the leaves were off and about half the bracts. After one month in the dwelling, all the colored bracts had fallen and only a few leaves were left near the top of the stems. The plant which received the solution of one atmosphere concentration continued in good shape for about two weeks. The smallest plant or the one which had received the solution of two atmospheres concentration at the end of four weeks had all the leaves still attached and, as well, some of the bracts. In addition, it had produced several new shoots. The poinsettia, we expect, will respond to the same treatment as was suggested for the sweat pea: dilute solutions to bring along the growth and then concentrated solutions to harden the growth.

A very striking example of practical commercial application is seen in the rhododendron. Large numbers of *Rhododendron ponticum* are grown for understocks in grafting hybrid varieties. It requires two to three years by common methods to produce, from seed, grafting size seedlings. Several years ago, a graduate student was working on the nutrient requirements of rhododendrons. This work was done in the laboratory of the Department of Plant Physiology under the direction of Dr. J. W. Shive, one of the foremost workers in this phase of physiology. In one year, the student was able to grow stock large enough to graft, planting the seeds in sand and using nutrient solutions. One plant at the end of two years and ten months stood about six feet high. Under ordinary methods it would have been only twelve inches or so high with a stem the thickness of a pencil. A year or so ago, a crop of seedlings were grown by this method and were shipped to a propagator. They were grafted, and the union took place just as readily as with stock grown in the usual manner and the plants are doing very well.

The application of the practice to the growing of house plants interests us, especially for the city house conditions. A hydrangea plant, grown in the field during the summer, was lifted, the soil washed from the roots and it was then placed in sand in a closed crock. It grew splendidly, producing large flowers. However, very soon after the bloom was off, the plant showed signs of injury. It is not easily possible to grow plants in sand in closed containers at present because of the need of flushing, mentioned above. This is a problem upon which we are working. However, whenever drainage is possible splendid plants can be grown. Blue-lace flowers, cinerarias, annual lupine and English ivy developed well. These were in ordinary burned clay pots with the drainage hole at the bottom to permit flushing.

Where the plants can be grown by means of constant drip, which requires a receptacle for waste leachings (which, by the way, can be used over and over again), remarkably fine plants can be grown. A small wooden bracket can be attached to the rim of the pot and the reservoir placed on this. In this type of culture a mason fruit jar, inverted in a dish, forms the reservoir. Even with what we term " slop culture," good plants can be grown. In this technique a pint of the solution is put on once or twice a week. Provision again must be made for drainage.

The sand culture of plants offers splendid opportunities for practical application. Commercially, it is possible to grow almost the entire range of cut-flowers. The commercial florist, however, is still skeptical, and with reason. He has been taught to believe that manure is necessary for the growing of plants. However, the florist is gradually adopting the use, in the greenhouse, of commercial fertilizers. So it is reasonable to believe that

as the advantages, both as to convenience and economic saving, of the method of culture in sand become known, it will be widely adopted. So far as the culture of house plants is concerned, it requires only that the method be made absolutely fool-proof and free from the present need for some messiness, and the plant lovers, especially in the city, will adopt it. Better plants can be grown, there is freedom from many cultural difficulties that make for disappointment. So, what was at first a very valuable tool in the laboratory, giving us information that has been of inestimable value in the solution of cultural problems and in giving us better understanding of cultural practices, seems in a fair way about to become a common practice in everyday horticulture.

TWENTY-FIVE YEARS OF HORTICULTURAL PROGRESS, WITH SPECIAL REFERENCE TO FOREIGN PLANT INTRODUCTION, 1910–1935

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In the early stages of its development, American horticulture was strongly influenced by the work of the amateur, but the past twenty-five years have witnessed a swing toward, and the development of, the commercial side of horticulture to a comparatively high degree of perfection. The last quarter of the nineteenth century saw the establishment of Land Grant Colleges and Experiment Stations; the past twenty-five years have seen their growth to a stage of organization and specialization which one would never have predicted in so short a time. From a small beginning in the latter part of the nineteenth century horticultural research in our experiment stations, stimulated by the demand of commercial horticulture for a solution of the problems which were continuously arising, reached a point in 1927 when there were slightly less than 2,000 research projects devoted to horticulture alone. Today there are over 1,000 horticultural projects, 555 on fruits, 358 on vegetables, 86 on ornamentals and 67 in which special emphasis is placed in a chemical or physiological study of plants representing all of these groups.

There has also been increased support for privately endowed research institutions as evidenced by the founding of the Boyce Thompson Institute for Plant Research, the increase in the facilities of the Brooklyn, Missouri, New York and other botanic gardens, the endowment of the Arnold Arboretum and the activities of plant scientists of the Smithsonian and Carnegie Institutions.

It is evident that as a result of the emphasis which has been placed on horticultural research and the development of related fields in fundamental sciences, principally physiology, genetics, cytology and biochemistry, we have acquired a much better understanding of the horticultural plants with which we have been working.

CHANGES IN THE TREND OF HORTICULTURAL PRODUCTION

The past twenty-five years have witnessed the development of highly specialized agricultural industries under irrigation in the western part of the

United States. The conspicuous development of the Pacific coast as a horticultural region, specializing in crops for which it is peculiarly adapted, has been one of the outstanding performances of American horticulture. Although perhaps not so spectacular, the trend in other parts of the United States also has been toward the perfecting of highly specialized areas of fruit production.

There are a number of reasons for this change in trend of horticultural production. Predominatingly agricultural in the early part of our national life, more recently we have rapidly changed to an industrial and commercial nation. Our population has undergone a change from rural to urban and hand in hand with it there has been a change in our food requirements giving us a diet more suited to the more sedentary life of the cities.

Horticulturists realize that even though much credit must be given to horticultural research workers for their influence in helping the industry to keep abreast with these changes, the discoveries in the field of human and animal nutrition have been a most important factor in influencing our national diet during this particular period. Credit must also be given to the men closely associated with the various horticultural industries for their foresight in coordinating the production of these industries and capitalizing on the findings of research workers through the improved agencies of advertising. These developments have given tremendous impetus to the production of vegetables as well as fruits. From relatively small greenhouse industries in the East, such crops as lettuce, cucumbers, and tomatoes have expanded until their culture in the higher altitudes of Colorado and Arizona, the mild winter valleys of California and the more favored spots in Texas, Florida and other southern states, has reached almost unbelievable proportions. It is extremely doubtful that such changes would have been possible if the work in the field of human and animal nutrition had not been performed.

In concentrating the production of individual crops, the horticultural industry opened itself up to more serious losses from plant diseases and insects. Much of the success in their control must be credited to the research work carried on in these particular fields. Environmental extremes such as low temperatures and drouths tend to limit the areas in which certain horticultural crops can be grown and sometimes injure the plants within these areas. We may continue to grow horticultural crops despite these conditions but it is becoming increasingly evident that control measures of diseases and insects and the use of semi-hardy or drouth resistant plants are but temporary expedients and until we develop plants that are adequately resistant to attacks of insects and diseases and more suitable for their environment we cannot hope to have a stable industry.

THE RÔLE OF PLANT INTRODUCTION IN THE DEVELOPMENT OF AMERICAN HORTICULTURE

It is interesting to note the part that plant introduction has played in the development of horticulture during this period. The common concept of plant introduction is that it constitutes the bringing in of some new and interesting plant such as the mango or the date, adding to the number of our successful commercial crops or in some sections replacing those which have reached the point where they can no longer be profitably grown. The average person loses sight of the fact that there is no short road to success and that all plant introductions, no matter how promising they appear in the native habitat, must prove themselves adaptable to this country and even then must overcome the severe competition of other crops, the production and marketing of which have become highly perfected.

There are exceptions, of course, for the past twenty-five years have witnessed the successful establishment of a date industry in the southwest which has proved itself economically sound. Likewise, the avocado, known to the Indians of Central America before the Spaniards came and first introduced in 1863, received its impetus for commercial development in Florida and California when the best of the hardy Mexican and Guatamalan varieties were sent in by Popenoe, Cook and others during the period between 1910 and 1920. We have now reached the stage where it is estimated that 20,000,000 pounds are consumed annually in the United States. The Methley, a dark red colored plum introduced from Natal, South Africa, has proved especially well adapted to the southern part of the United States, is one of the leading plum varieties grown in Texas and when in season can be purchased on many of our northern markets. The Quetta nectarine, a clingstone variety of excellent appearance and quality originating from a small collection of nectarine seeds from India, has demonstrated its fitness as a shipper and has taken its place on our eastern markets as one of California's new commercial fruits. Over six thousand soybean varieties, types and strains have been introduced from the Orient. These introductions, and strains developed from them, have extended the culture of this crop from 50,000 acres in 1907 to 4,000,000 acres in 1932 and today one of our largest automobile manufacturers calls attention to the fact that soybean oil is one of the main ingredients of the enamel used in painting his cars.

Other introductions such as the Chinese jujube and Japanese persimmon, although creating considerable interest when first introduced, have not found sufficient favor with the consuming public to warrant commercial expansion. However, they are worthwhile additions to the fruits of this country. Still

others such as the mango, the litchi, the tung oil and pistache nut, important economic fruits in other countries are under test at the present time.

These represent only a few of some 69,000 plant introductions which have entered the United States during the past twenty-five years, among which there were many horticultural representatives. Of what value are the others?

With increased knowledge of plant response there has come a greater appreciation of the value of plant introductions to the solution of horticultural problems when utilized by our plant breeders. This is clearly illustrated by some of the more recent accomplishments in this field. As a result of the research work which brought out the nutritional value of spinach, the production of this crop has been greatly stimulated until at the present time the respective shipments from Texas and Virginia, the two states which produce the bulk of the crop, amount to 7,000 and 2,500 carloads annually. Early in the development of this crop in Virginia a mosaic disease (blight) appeared and threatened to seriously curtail the growth of spinach in that state.

The late Frank Meyer while exploring for plants in Manchuria in 1908 became interested in a strain of spinach which was native to that country and included seed in his plant collections which he sent back to America. It proved to be of relatively little commercial value and remained comparatively unknown until research workers at the Virginia Truck Experiment Station began testing it along with other strains of spinach in an effort to find a blight resistant type which could be used in their breeding work. It was found blight resistant and when crossed with the Savoy-leaved or Bloomsdale variety, a blight resistant strain of high quality, the Virginia Savoy was produced which is used as a fall crop in sections where blight appears. Later another blight resistant variety, Old Dominion, was produced by crossing Virginia Savoy and King of Denmark varieties, this new variety being adapted for spring planting. That this Manchurian spinach was available was more or less accidental for at the time of its introduction the problem of developing a blight resistant spinach had not presented itself.

Another example of a successful search for disease resistance in introduced plants is illustrated in the recent melon work which has been carried on cooperatively by the University of California and the United States Department of Agriculture. One of the largest melon growing industries in the world is located in the Imperial Valley of California and due to the limited rainfall, high temperatures and resulting low humidity most of the diseases which attack melons in humid areas are not a factor there. In 1926 powdery mildew appeared in the field and in that year and again in 1930 yields were reduced 30 per cent or more and the quality of the melons on the remaining

vines was lowered, creating considerable concern in the minds of those who were responsible for the reputation of these melons on our markets.

In 1926 investigations were started in an effort to breed mildew resistant varieties to replace those grown in the valley. The first problem was to find melons with the necessary resistant qualities and with this in mind melons were introduced from all parts of the world and tested with all commercial varieties for mildew resistance. Seed obtained from India in 1928 gave numerous plants practically free from mildew when grown in rows adjacent to varieties the vines of which were practically all killed. Since that time other mildew resistant varieties have been introduced from Asia. The fruits of the mildew resistant melons were of no commercial value since they had a very low sugar content, unpleasant flavor and no shipping quality; however, the mildew resistance of these melons was combined with the eating and shipping qualities of our good commercial varieties, and strains were developed similar to the Hales Best type. At the present time these are being brought to perfection for commercial use and it is entirely probable that within a few years the mildew spectre will no longer worry the melon grower in that section.

Similarly in the case of watermelons, the industry has had to combat a serious wilt disease and thousands of dollars have been appropriated for its study. Here again seed from foreign sources was found to carry the factor of wilt resistance and even though the resultant melons were inedible themselves, furnished research workers in Iowa with excellent material for the development of disease resistant types. The economic significance of this work is more readily appreciated when one realizes that there are over 200,000 acres of watermelons grown in this country every year, representing a $12,000,000 industry.

Although there is not sufficient time to give a detailed description of recent plant exploration work for disease resistant potato species, no discussion of the economic value of this type of work would be complete without mentioning it, since it concerns a $250,000,000 industry. With the aid of wild *Solanum* species collected in Central Mexico in 1930, Doctor Reddick of Cornell has already made considerable progress in his attempts to develop blight resistant potato varieties.

Research workers have been equally successful in their attempts to develop varieties to take the place of those which are more or less susceptible to serious insect injury. As an illustration mention might be made of the work which has been done at the University of California by those responsible for the problems which arise among the vegetable growers of that state.

In 1933 the 80,000 acres of onions produced in this country represented a $13,000,000 industry and California produced about one-eighth of this crop.

In an effort to combat thrips insects which were difficult to control because of their habit of breeding and working in the axis of the leaves, Dr. H. A. Jones and his associates conceived the idea of breeding a variety, the growth habit of which would hinder the development of thrips and make it easier to control those that did appear. Previous success in finding the right kind of breeding material for other problems among introduced plants suggested foreign countries as a possible source for the onion plants they had in mind for this work. It so happened that the Division of Plant Exploration and Introduction of the Department of Agriculture was sending an expedition to Russian Turkestan and Iran, known at that time as Persia, and a search for suitable onion types in this section of the world was included in the program of the expedition. Among the onion varieties brought back from Iran, one, later named the White Persian, not only proved to be exceptionally thrips resistant but has contributed materially to the successful development of new thrips resistant strains which may go a long way in solving the problem of controlling onion thrips which investigators have worked on for three-quarters of a century or more.

That research workers are becoming more appreciative of plant introduction work is illustrated by the fact that in 1928 upon inquiry among the horticultural research workers in the United States it was found that very few felt the need of introduced plant material in the solution to their problems yet today the United States Department of Agriculture, through its Division of Plant Exploration and Introduction, is attempting to secure specific plant material for use in some 200 or more of these horticultural projects.

Most of the emphasis of the research work during this period has been placed on fruits and vegetables but it is interesting to note that investigators are turning their attention to ornamentals. The recent California work in producing rust resistant varieties of the cultivated snapdragon is an example. Although rust resistance was secured from domestic types, and the aid of foreign material was not needed in this case, it is interesting to note that in a collection of snapdragon species originally secured in Spain by the late Dr. E. Baur of Germany and through his courtesy later introduced into this country, there were five which showed complete immunity.

Although many of our ornamental introductions were made by Meyer, Wilson, Fairchild, Rock and others in the early part of the nineteenth century, their value to horticulture has been demonstrated during the past twenty-five years. The beautiful *Juniperus squamata Meyeri* and *Juniperus chinensis* have been used extensively in our evergreen plantings; the lovely Chinese holly, *Ilex cornuta* has demonstrated its value for the gardens in the warmer sections of the United States; *Rosa odorata,* a Chinese wild rose, has given us

an excellent rootstock for greenhouse culture and *Rosa hugonis,* a beautiful yellow rose sent to us by Kew Gardens, has become a valuable addition to our rose collection. The fast growing Chinese elm, *Ulmus pumila,* has proved particularly valuable in the Great Plains area, either as a shade tree or in mixed windbreak plantings and last but not least varieties of flowering cherries introduced in the early part of this century have had an opportunity to develop and demonstrate their beauty. These are but a few of the ornamental introductions which we have been adding to our gardens during the past twenty-five years. The most striking development in this field has been the vast interest which the American public as a whole has shown in ornamental plant material. This is evidenced in the increased number of garden clubs, publications and plant breeders in this field.

In conclusion it may be said that although it is difficult to present a complete picture of horticultural progress during the past twenty-five years, its interdependence on all agencies is clearly illustrated.

MODERN METHODS OF PLANT PROPAGATION

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The subject assigned to me calls for a report on propagation by seeds and vegetative methods. The latter should be divided into propagation by grafting and cuttings. I shall, however, omit further reference to grafting and I shall give only a short review of progress in propagation by seeds.

Seed germination and propagation. Before 1906 seed types which did not germinate readily were classed under one of two categories:

a. Delayed germination due to hard seed coats.

b. Delayed germination due to dormant embryos.

The first type was thought to be benefited by freezing and in practice seeds were sown or stratified in the fall of the year so they could be frozen. Seeds with dormant embryos were commonly called two-year types. They were planted in the spring and the seedlings appeared the following year.

We now know that freezing does not aid in seed germination and is frequently harmful; that most of the so-called two-year types can be handled in such a way as to force seeds to germinate whenever it is most desirable. Investigations in this field have gone further to influence practice than most any other type of research. Through the efforts of Dr. William Crocker, director of the Boyce Thompson Institute, his former students, and his associates during the past 25 years, many uncertainties in connection with handling of seeds for plant production have been eliminated. Much of the progress has been due to the following discoveries:

a. Dormant embryos can be after-ripened and prepared for germination by subjecting the seeds while in moist medium to low temperature. The time and temperature requirements vary with the seed types. For example, the seed from *Cornus florida* will not germinate if planted directly from the ripe fruit or if stored dry, but if stored in a moist medium for 100 days in a temperature range of 33° to 41° F., they germinate readily when planted.

b. Some types, like barberry, are benefited by alternating temperatures such as occur naturally outside in the spring of the year.

c. Types like *Viburnum* have dormant epicotyls though the hypocotyls will develop. In this case, the seedling first establishes a root system at grow-

acid, and α-naphthylacetonitrile. These compounds used in lanolin as described by Hitchcock (1) for β-indolylpropionic acid cause initiation of roots where applied to leaves or stems. Plates I and II give some idea of their effectiveness. In addition to the effect on root production, all sixteen of the known growth substances cause local acceleration in growth of tissue causing swelling and bending of stems, and epinasty of leaves.

The results obtained with known chemical compounds lend support to the theory that plants produce growth regulating substances. Perhaps the amount occurring in the different plants determines the response a vegetative organ can make when separated as a cutting.

In arranging for my part on the program, Dr. Gager asked me to say a word looking to the future. The most hopeful things now in sight come from results with these new growth substances. Root-forming substances are now a reality. Perhaps sometime we shall know shoot-forming and flower-forming substances. With proper methods developed, we should soon be able to provide amateurs with the necessary chemical compounds and instructions to greatly facilitate vegetative plant propagation.

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PLATE I, *A* AND *B*. The root-forming capacity of indolebutyric and α-naphthaleneacetic acid.

A. Left, control; right, 0.01 per cent indoleacetic acid injected by means of glass tubes drawn to capillary size at one end. Photographed 14 days after injection.

B. Left, control with top removed and pure lanolin applied to cut surface; right, plant with top removed and then cut surface treated with 1 per cent α-naphthaleneacetic acid in lanolin. Photographed 8 days after treatment.

PLATE II, *A*, *B*, AND *C*

A. Roots initiated locally on tobacco stem from application of 3 per cent phenylacetic acid in lanolin.

B. Initiation of roots along the stem of tobacco plant induced by 0.2 per cent solution of indolebutyric acid in water. The substance was admitted by immersing an overhanging slit stem piece in a glass vial containing the solution.

C. Buckwheat cuttings showing the effect of root-forming substances. Left, two controls showing normal basal rooting while growing in Knop's solution; middle, two cuttings growing in Knop's solution containing 0.001 per cent indolebutyric acid; right, same as middle except solution contained only 0.0001 per cent of the substance.

PLATE I.

ZIMMERMAN—PLANT PROPAGATION.

PLATE II.

ZIMMERMAN—PLANT PROPAGATION.